FISHERIES RESEARCH BOARD LIBRARY

JOURNAL

OF THE

FISHERIES RESEARCH BOARD OF CANADA

Volume 26, No. 3

6-12

OTTAWA
OCT 1969

CONTENTS

	Pages
G. HUNTSMAN — An appreciation. By J. L. HART.	255–258
WILIMOVSKY, NICHOLAS J. Rare skates of the Newfoundland and neighbouring areas	259–279
KASSWELL, C. J. KASSWELL, AND C. J. KASSWELL. Effects of light on growth of oysters, mussels and quahaugs	281–288
HARDISTY, M. W., I. L. HART, AND KAYE HAYASHIDA. Comparative toxicity of the intraperitoneal alimentary tract of parasitic and nonparasitic lampreys from the Great Lakes region	289–306
HOPKINS, T. L., AND A. G. COBURN. Nucleotides and related compounds, sugars, and homarine in shrimp	307–311
BOURNE, NORM. A comparison of catches by 3- and 4-inch gauge on offshore scallop drags	313–333
HOUSTON, STUART JR. Adjustment of buoyancy in young Atlantic salmon and brook trout by changes in swimbladder volume	335–352
LEMMENS, C. H. J. Drift bottle observations in Northumberland Strait, Gulf of St. Lawrence	353–368
FRASER, A. R., AND C. W. ANDERSON. Effect of photoperiods on the behavior of juvenile Atlantic salmon (*Salmo salar* L.) in vertical and horizontal light gradients	369–383
GLEESON, D. W. Survival of lobsters, *Homarus americanus*, out of water	385–394
SUPPERS, J. W., AND H. W. SMITH. Changes in a stream population of trout associated with increased silt	395–404
HOLETT, J. R., AND D. B. SUTHERLAND. Respiratory metabolism of pumpkinseed (*Lepomis gibbosus*) in relation to swimming speed	405–409
MACCARTHY, W. A., DOROTHY A. CHALKER, E. J. LAUZIER, W. J. DYER, AND D. R. IDLER. Studies on the quality of Newfoundland cod. 10. Effect of some commercial freezing rates on the frozen and stored quality of cod	411–420
SCARRATT, D. J., AND P. E. FOWLER. Preliminary trials of a tag for salmon and lobsters	421–423
SPRAGUE, J. B., AND R. ANN RANDALL. Lethal levels of mixed copper-zinc solutions for juvenile salmon	425–432

(*Continued overleaf*)

OTTAWA
MARCH
1969

SCHWARTZ, D. E. Migrations of harp seals *Pagophilus groenlandicus* (Erxleben) in the Northwest Atlantic 433–464
FLEMING, A. M. Trends in catch, age, and size of cod from the commercial longline fishery at Bonavista, Newfoundland, 1953–62 465–474
RICKER, W. E. New records and descriptions of Plecoptera (class Insecta) 475–501
ODULVIE, D. M., AND J. M. ANDERSON. Effect of DDT on temperature selection by young Atlantic salmon, *Salmo salar* 503–512
NIXON, J.A.C. Retinomotor changes in flatfishes 513–520
PALOHEIMO, J. E., AND L. M. DICKIE. Food and growth of fishes. I. A growth curve derived from experimental data 521–542
GRAINGER, E.H. Zooplankton from the Arctic Ocean and adjacent Canadian waters 543–564
FOWLER, P.M. Life history and ecology of American plaice (*Hippoglossoides platessoides* F.) in the Magdalen Shallows 565–598
BLAIS, A.A. Bay of Islands and Humber River Atlantic salmon investigations 599–620

NOTES

Seasonal distribution of monkfish along the Canadian Atlantic mainland. By YVES JEAN 621–624
Canadian Atlantic salmon recaptured near Greenland. By R.L. SAUNDERS, C.J. KERSWILL, AND P.F. ELSON 625–629
Ancient Canadian east-coast oyster and quahaug shells. By J.C. MUDGE, ARTHUR H. CLARKE, JR., AND JOHN S. ERSKINE 631–634
Are killifish poisonous? By H.C. WURTS, J.C. MUDGE, AND L.R. DAY 635–638
Lesions on the abdominal membrane of lobsters. By D.W. MCLEESE 639–640
Recent articles 641–642

Editor:

J. C. STEVENSON

Associate Editors:

E. G. BELIGH AND G. L. PRITCHARD

Fisheries Research Board of Canada
Sir Charles Tupper Building
Ottawa, Ont., Canada

Manuscripts for publication should be addressed to the Editor

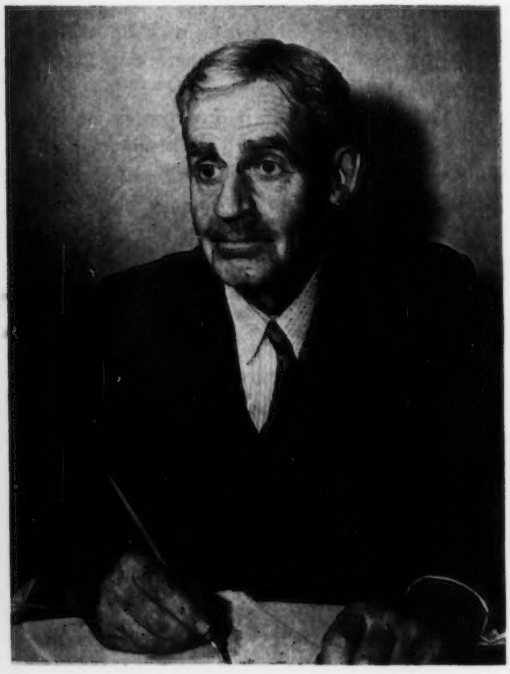
ROGER DUHAMEL, F.R.S.C.
QUEEN'S PRINTER AND CONTROLLER OF STATIONERY
OTTAWA, 1965

A. G. HUNTSMAN — An Appreciation

Iron sharpeneth iron; so a man sharpeneth
the countenance of his friend. — PROVERBS 27: 17

This issue of the Journal of the Fisheries Research Board of Canada recognizes Doctor Archibald Gowanlock Huntsman and the part he has played in developing fisheries science, in training students and in fashioning the Fisheries Research Board.

Dr Huntsman was born in Tintern, Ontario, on November 23, 1883. His father was Lution Erotas Huntsman and his mother the former Elizabeth Gowanlock. After receiving his early education at local schools, and St. Catherines Collegiate Institute, where he acquitted himself with distinction, he entered the University of Toronto in 1901 with a matriculation scholarship. Dr Huntsman received his Bachelor of Arts degree in 1905. He then continued on to earn his Bachelor of Medicine in 1907, to which the University added the MD degree in 1933; but he never practised medicine. In 1916 he was elected to Fellowship in the Royal Society of Canada.



In 1908 Dr Huntsman married Florence Marie Stirling who has been throughout the years his staunch supporter and patent admirer. Their three daughters reflect well the advantages of a home where intellectual curiosity was a condiment to the more normal fare of life.

In 1904, Dr Huntsman went as a senior student to the Georgian Bay Biological Station at Go-Home Bay operated under the Board of Management of the Marine Biological Station. (The Board of Management was later replaced by the Biological Board of Canada, and, in 1938, it in turn became the Fisheries Research Board of Canada.) From 1904 until his retirement in 1953 Dr Huntsman's career was identified with the activities and growth of the Fisheries Research Board and its predecessors. In 1904 his assignment at Go-Home Bay involved the flora of

J. FISH. RES. BD. CANADA, **22**(2), 1965.
Printed in Canada.

the area and the life history of black bass. In 1905 he was back again and continued there in the summers through 1907. In the summers of 1908 and 1909 he was on the Pacific Coast based on the newly established Biological Station at Departure Bay near Nanaimo. His assignment was to make a general collection of marine animals for the University of Toronto and to make a special collection of tunicates for systematic study. The study of tunicates as well as other forms was continued in 1910 at the St. Andrews Biological Station. In the summer of 1911 he returned to the St. Andrews Station to take charge, replacing Professor D. P. Penhallow who had died in the previous autumn. He was Curator from 1911 to 1913 and again from 1916 to 1919. In 1919 he was appointed Director, a position he held until 1934. From 1924 to 1928 he had the added responsibility of the directorship of the Biological Board's newly established Fisheries Experimental Station in Halifax. In 1934 he became Editor and Consulting Director for the Board. He carried his responsibilities as Editor until 1949 and as Consulting Director until 1953. During all of this period Dr Huntsman was associated with the Department of Biology of the University of Toronto as: Assistant (1905–07), Lecturer (1907–16), Associate Professor of Marine Biology (1917–27), and Professor of Marine Biology (1927–54).

During the 1920's and early 1930's Dr Huntsman directed much of his effort to the herring fisheries in the Bay of Fundy region. He played an active part in the investigation of possible effects on fisheries there of constructing a series of dams across the entrance of Passamaquoddy Bay in such a way as to facilitate development of hydroelectric power. This work nourished his continuing interest in the subject of what makes fisheries.

Dr Huntsman has a longstanding interest in salmon research. When relieved of his major administrative responsibilities in 1934, he directed much of his effort to studies of Atlantic salmon with emphasis on the effects of the environment on movements and behaviour. This led to the concept of biapocrisis — the response of the entire animal to its surroundings, which he often emphasizes. From 1935 to 1946 he directed all the Board's Atlantic salmon research and laid the philosophical foundation for much of the objective and quantitative work which followed, including investigations on the effects of predation, and studies of young.

Dr Huntsman does not believe that science should develop in a vacuum. He has many affiliations with learned societies and other organizations. However, he is no mere joiner. He took an active part in the societies of his choice. That he did not shirk administrative responsibilities is shown in the following summary: Corresponding Member of the American Museum of Natural History; Foreign Honorary Member of the American Academy of Arts and Sciences; Fellow of the American Association for the Advancement of Science; Member of the British Association for the Advancement of Science and Vice-President of Section D in 1924; Member of the North American Council on Fishery Investigations from 1929 to 1939, Secretary 1922–38, and Chairman 1938–39; Member and Secretary of the Board of Inquiry for the Great Lakes Fisheries 1940–42; Member of the Board of Trustees for the Bermuda Biological Station for Research, Inc., Vice-President 1935–54, and in 1963, Patron (Hon.); Honor-

ary Trustee of the Woods Hole Oceanographic Institution; Member of the Royal Canadian Institute, and Honorary Librarian 1920–25; Member of the American Fisheries Society, and President 1936–37; Member of the American Society of Zoologists; Member of the Ecological Society of America; Member of the American Society of Limnology and Oceanography, Inc.; Member, and later Honorary Member, of the Nova Scotian Institute of Science; Member, first President, and since, Honorary President, of the Ontario Society of Biologists; Honorary Member of the Canadian Society of Zoologists; Honorary Member of The Wildlife Society; Honorary Member of the Marine Biological Association of the United Kingdom; President of Section V (Biological Sciences) of the Royal Society of Canada 1924–25, and President of the Society, 1937–38. In 1952 Dr Huntsman was awarded the Flavelle Medal of the Royal Society of Canada in recognition of his outstanding contribution to biological research in Canada.

It is appropriate to note that Dr Huntsman's heavy burden of administrative, research, and society responsibilities was borne by a man who was continually subject to ill health and sometimes was unable to operate normally.

Officially Dr Huntsman retired from the Board's service in 1953 and from his professorship with the University of Toronto in 1954. However, these administrative details produced little difference in his manner of life. At a dinner honouring Dr Huntsman in connection with his retirement from the Board's service, the late Dr Stewart Bates, Deputy Minister of Fisheries, said: "Dr Huntsman's retirement later this year will leave a gap. But to-night I cannot think of him as really retiring. I have an appointment with him to-morrow morning that will probably launch a new project. . ." We are not privy to the outcome of that meeting but it is certain that Dr Huntsman did not retire into inactivity. Many of his advisory responsibilities remained and were pursued with renewed vigour. And to paraphrase the late Dr William Rowan's presentation of Dr Huntsman for the Flavelle Medal, he continued as "an inveterate attender of meetings who pops up incessantly to offer opinions and criticisms. His remarks are always kindly and constructive: he exhibits a rare combination of broad knowledge and philosophical outlook. As a contributor to original thinking, although not always unanimously agreed with, he stands as a unique, influential, and courageous figure in the world of Canadian biology." He has continued his interest in debate and fostered various discussions on all sorts of subjects. During the winter of 1963–64 he initiated a series of meetings to urge re-orienting academic instruction toward emphasizing the study of the animal in its environment. He will never retire.

A. G. Huntsman was, and is, the great stimulator. He is the provocative thinker whose habit of mind is to challenge any positive statement. He challenges word meanings. He challenges basic concepts. He challenges practically everything. He believes in debate as a process in group thinking and he is amazingly adept both in guiding group discussions when he so chooses, or in having his views prevail in argument. Sometimes this faculty irritates his associates but there is no question but that they benefit from his polemics. That the value is recognized is attested by the acceptance and success of discussion groups he

organized at Board meetings, at the St. Andrews Station, within the Royal Society of Canada, and among graduate students at the University of Toronto.

Dr Huntsman's interests are eclectic indeed. A cataloguing of his many publications requires such varied headings as: ascidians, other invertebrates, salmon, marine fish other than salmon, fishes in general, fish technology, limnology, oceanography, limiting factors for marine animals, philosophy. It is told that when he took charge of the St. Andrews Station in 1911, the Board's Chairman gave him a list of eleven problems from which young Curator Huntsman could select a project for off-season research. There was surprise mixed with admiration the next spring when he submitted reports on all eleven subjects, and it became clear that the intention was misinterpreted. The mistake may have set a pattern. Throughout his career, Dr Huntsman's opportunities and energy for testing hypotheses seldom kept up with the explanations of natural phenomena his probing mind contrived. As a result he often failed to stay with one subject beyond the time necessary to support his explanation. When his curiosity was satisfied and he found his ideas consonant with other facts, he was on to the next aspect of the problem he was attacking without compiling or, at any rate, presenting enough objective evidence to convince critical minds. However, his published papers and reports, and his dissertations have led to critical appraisal of entrenched ideas; they have stimulated new research; and they have opened new avenues of thought.

Dr Huntsman's versatility does not stop with biology. For four years he was Director of the Board's Technological Station in Halifax and his contributions there rival those he made through the St. Andrews Biological Station. It was at Halifax that he pioneered work on fresh frozen fillets as a method of marketing better quality fish. It was there also that he first explored and tested refrigerated brine and jacketed cold storage for holding fish in good condition. All of these projects were thirty years ahead of their time.

Environment plays a dominant part in shaping a career. Dr Huntsman himself has said, "... I am, scientifically, a product of the Board and what it represents. I merely responded to the stimuli I faced in associations with the fine men who had the vision of the Board's work (particularly Wright, MacCallum, and Knight) and with the investigators, administrators, fish merchants, and (not least) the fishermen. I mention specially Dr Johan Hjort, to whom I was assigned as an assistant in 1914 and 1915, and who brought to our waters the European vision of oceanic exploration."

Dr Huntsman had a special talent for extracting the maximum amount of research from the dollar allotted for his use. In days of small budgets this was an important factor in enhancing the reputation of his Station and the Board. In a real sense he can be said more than anyone else to have given the Board an international reputation. The results of his direction, his stimulation, and his economies live on in the intellects and accomplishments of many scientists in many fields of research throughout the continent. The papers in this issue of the Journal have been prepared by some of those he has influenced.

J. L. HART

Rare Skates of the Newfoundland and Neighbouring Areas[1]

By Wilfred Templeman

Fisheries Research Board of Canada
Biological Station, St. John's, Nfld.

CONTENTS

	Page
Abstract	259
Introduction	259
Raja erinacea Mitchill 1825 — Little Skate	260
Raja hyperborea Collett 1879 — Arctic Skate	262
Raja jenseni Bigelow and Schroeder 1950 — Jensen's Skate	264
Raja lintea Fries 1838	265
Raja mollis Bigelow and Schroeder 1950	268
Acknowledgments	270
References	271
Tables I–V	272

ABSTRACT

Raja erinacea is reported from the east coast of Newfoundland, a first record from the Newfoundland area. *Raja hyperborea* is recorded from east of Baffin Island, 60 nautical miles south of the most southerly previous record on this coast. *Raja jenseni* and *Raja mollis* have been found on the southwest slope of the Grand Bank, and *Raja mollis* on the continental slope off northeast Newfoundland and Baffin Island. These are northward and eastward extensions of range from the southern part of the Nova Scotian Shelf. Two individuals of *Raja lintea* are recorded from Flemish Cap, the first record of this species west and south of West Greenland. Body proportions and other characteristics of the rare skates are discussed in relation to those reported by previous authors.

INTRODUCTION

Largely as a result of the otter-trawling operations of the *A.T. Cameron* in recent years for redfish, new information has been obtained on the distribution of the skates of the Northwest Atlantic. A No. 41 otter trawl with a 24-m headrope was used and trawling was carried out at fishing stations on lines extending across the continental slope usually from about 180 to 730 m (100–400 fath). Only the relatively scarce or new species found in Newfoundland or neighbouring waters are considered here. Three of the skates recorded in this paper (*Raja erinacea*, *Raja jenseni*, and *Raja mollis*) have not previously been recorded from the Newfoundland area and *Raja lintea* has apparently not been previously recorded from the western Atlantic west or south of West Greenland.

Measurements for body proportions were taken generally as by Bigelow and Schroeder (1953a) in a horizontal line at right angles to perpendicular

[1]Received for publication August 21, 1964.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

planes at given points. The snout length in front of mouth is the direct distance. The distances from snout to the orbits and to mid-pupils were taken over the surface of the head to the mid-line between these paired structures. The mouth breadth in our measurements is the width as it appears normally in ventral view and not that obtained by searching deeper for the exact width of the mouth. All rows of teeth were counted, even when, as sometimes happens at the ends of the series of rows, there was only 1 tooth of the row present. The number of rows in each jaw is referred to in the text as the tooth count.

RAJA ERINACEA MITCHILL 1825 — LITTLE SKATE

Distribution

Raja erinacea has been reported from the lower St. Lawrence River and the southern shore of the Gulf of St. Lawrence, including Chaleur Bay, southward to Virginia (Huntsman, 1922; Vladykov and McKenzie, 1935; Bigelow and Schroeder, 1953a,b). It is usually more plentiful in water shallower than 33 m. It has not been recorded previously from the Newfoundland area or further northward.

An immature male *R. erinacea* 201 mm total length was taken by Mr A. M. Fleming at 2–4 m depth in a beach seine haul at Bristol's Hope Cove, Conception Bay (Fig. 1, 2). A somewhat similar skate, *Raja ocellata*, is found in the southern part of the Newfoundland coastal area but no specimen of *R. erinacea* has previously been recorded. Although we have obtained only 1 specimen of *erinacea* few collections have been made in the inshore shallow waters of the Newfoundland area where this skate might be expected to be found.

Body Proportions and Other Characteristics

The specimen was recognizable by its general body proportions and median dorsal spine number (27) and general spine arrangement as being either a young *R. erinacea* or *R. ocellata*.

At the smaller sizes *R. erinacea* is apt to be confused with *R. ocellata* unless attention is paid to the tooth count, 38–64/38–64 (never more than 66 and usually less than 54) in *erinacea* and 72–110/74–110 (usually 90–100) in *ocellata* (Bigelow and Schroeder, 1953a). However, the tooth count in the Newfoundland specimen was 54/50 which placed the specimen within the tooth-count range of *erinacea* and well below that of *ocellata*.

A photograph of this skate with relevant tooth count and other information was sent to Mr W. C. Schroeder who confirmed the identification of the skate as *erinacea*. *Erinacea* is apparently much less plentiful in this area than *ocellata*. (Body proportions have not been presented for this specimen of *erinacea* since it is not to be expected that its body proportions would distinguish it from an *ocellata* of similar size, the only skate with which it can be confused.)

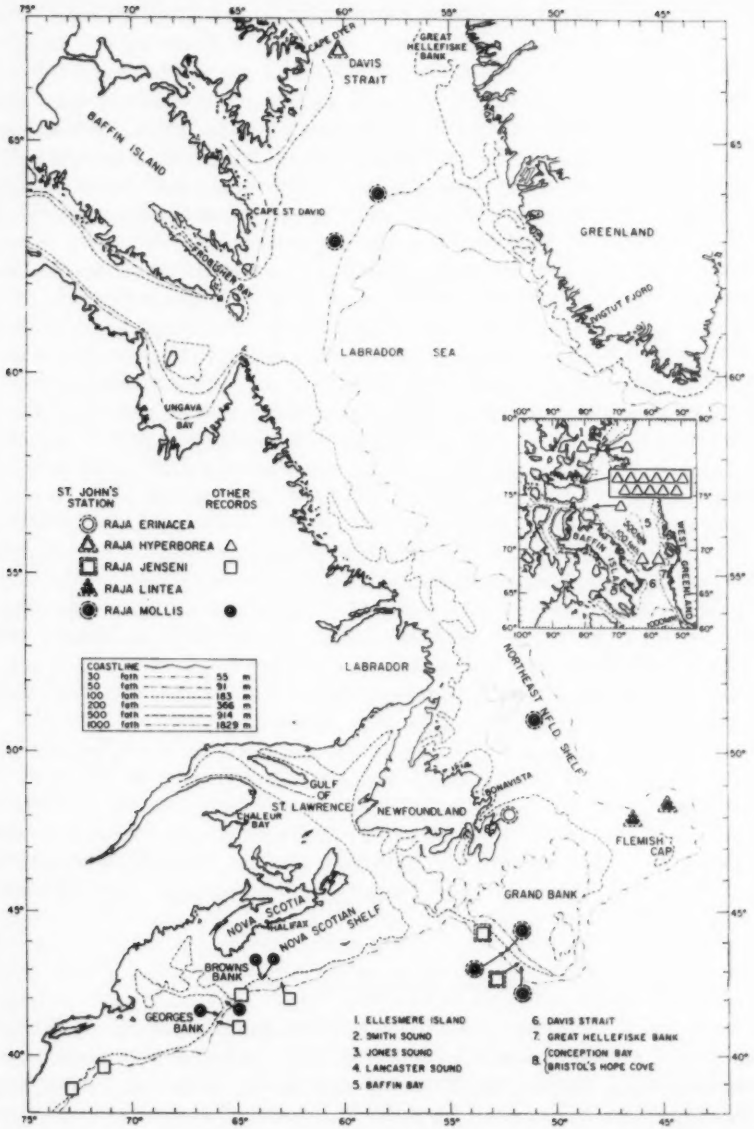


FIG. 1. Distribution in the western North Atlantic west and south of the West Greenland Shelf of all known records of *Raja hyperborea*, *Raja jenseni*, *Raja lintea*, and *Raja mollis*. (The location of the single Newfoundland record of *Raja erinacea* is also included. Because the outlines of the slopes of the banks are not always correctly defined and listed positions, especially from earlier years, may not be completely accurate, some of the indicated depths of records in the figure are not the same as those of the tables.)

RAJA HYPERBOREA COLLETT 1879 — ARCTIC SKATE

Distribution

Raja hyperborea ranges in deep cold water from the eastern part of the Barents Sea to the western side of Baffin Bay (Clark, 1930a; Jensen, 1948; Bigelow and Schroeder, 1953a). Sixteen specimens have been recorded by Jensen (1948) as taken by the Godthaab Expedition from the Canadian side of Baffin Bay (Fig. 1; Table I). (No. 1 and 2 of this Table could equally well be considered as West Greenland specimens.)

In our many years of operating research vessels in the Canadian area with many otter-trawling sets as deep as 730 m only one individual of this species has been recorded. This was taken by the otter trawl of the *A.T. Cameron*, from the extreme southern part of Baffin Bay, off Cape Dyer in 550 m, bottom temperature 1.16°C (Fig. 1, 3; Table I). This record is about 60 nautical miles farther southward than any previous record from the Canadian side of the Atlantic. The lack of records still farther southward along the Baffin Island, Ungava, and northern Labrador area and in many cruises to southern Labrador with sets from 180 to 730 m show that *R. hyperborea* must be scarce or absent in this area down to 730 m. (For three of these cruises by the *A.T. Cameron* as well as the above cruise to Baffin Island, etc. (Templeman, 1961) the author was in charge and examined every skate.)

This skate occurs at depths of 200 to at least 2390 m and in low temperatures, from 1.5 to −1.3°C (Bigelow and Schroeder, 1953a; Jensen, 1948). In West Greenland fjords and in Baffin Bay recorded temperatures for the occurrence of *R. hyperborea* are usually below 1°C (0.73 to −1.29°C for all the records of the Godthaab Expedition in Baffin Bay).

Raja hyperborea grows to a length of at least 870 mm (Jensen, 1948) but the largest thus far recorded from the Canadian side is 450 mm. The length of our specimen (Table I, No. 17, 157 mm fresh, 145 mm preserved) is slightly less than that of the smallest individual of this species previously recorded (160 mm; Thielemann, 1922; Bigelow and Schroeder, 1953a) and implies recent hatching from an egg case and the presence in the locality of a mature female.

Body Proportions and Other Characteristics

The body proportions of our small Baffin Island specimen (Table II) are somewhat different from those of the adult individuals of Bigelow and Schroeder (1953a). Part of the difference can be traced to the greater length of the tail posterior to the rear end of the 2nd dorsal. However, if the measurements are adjusted by a correction factor based on the average of this distance in the two specimens of Bigelow and Schroeder many of the body proportions are brought into line with those of the adult. Even when this is done the whole tail is longer in the young than in the adult. (In this regard Bigelow and Schroeder (1953a) say that for this species the tail length from the centre

of the cloaca to the 1st dorsal is about 77–82% of the total length in small specimens and about 54–57% in large individuals.) Thus the disc length and length from snout to centre of cloaca in our specimen are shorter and the tail length longer, even when corrected for extra length at the tip of the tail. On the other hand, if the tail were reduced to 42.7% of the total length as in the adults, instead of 52.4% in our uncorrected and 49.3% in our corrected total lengths, some of the body proportions would become greater than in the adults and others would approach more nearly to those of the adults. Since the tail gradually shortens from young to adult and body proportions are usually calculated as percentages of total length, their range can only be expected to be narrow when individuals of the same size and stage of maturity are compared. In order to reduce differences between young and adult for measurements not involving the tail, a better base for comparison might be disc length or the length from snout to end of pelvic fin. All measurements involving the tail would of course vary greatly with size of individual but this should be better than to have all measurementsg reatly affected by the wide differences in relative tail length with size.

Our small 145-mm specimen from Baffin Island is, however, generally similar in body proportions to the small and recently liberated 178-mm specimen of *hyperborea* from the Northeast Atlantic (Koefoed, 1927; Table II). Both of these specimens still had some trace of the origin of the yolk-sac remaining. Koefoed's specimen has a proportionately longer tail than that from Baffin Island, indicating that it may have been more recently out of the egg case, and because of its larger size has presumably come from a larger egg case and a larger female parent *hyperborea*.

The only northern skate with which our small *R. hyperborea* might be confused is *Raja radiata*. Tooth count, with a 38–44 range above and below for *hyperborea* and 36–46 for *radiata* (Bigelow and Schroeder, 1953a), offers no means of separation and in any case our individual with a 33-tooth count above and 34 below is outside the expected range. Very young skates may have a smaller number of rows. However, the 24 mid-dorsal spines in front of the 1st dorsal separate the species from *radiata* whose range for number of median spines is 11–19, the higher numbers being found in the north. Our example of young *hyperborea* differs greatly from young *radiata* of the same length which have bigger mid-dorsal spines, large spines on the pectorals instead of the tiny spines of our specimen, a much narrower disc width (61 and 63% of total length in two 151- and 150-mm specimens of *radiata* measured compared with 72% in our individual of *hyperborea*). Also, in young *radiata* the anterior edge of the pectoral is almost straight from just in front of the eyes to the outer tip, whereas the young *hyperborea* has the mature shape with a deeply indented pectoral curve in this region. (In this regard see the small *hyperborea* in Günther (1887, pl. 4) showing the deeply curved indentations in the anterior borders of the pectorals.)

The dorsal colour in this species ranges from dark grey to grey brown but on the lower surface the colour is more variable from mainly white with sym-

metrical dark markings to mainly dark with symmetrical white markings. Small individuals may be entirely white below or may have a number of small dark areas on disc, pectorals, and tail (Jensen 1914, 1948; Bigelow and Schroeder, 1953a).

Our small individual is brownish grey above. The ventral surface is mainly white with pale dark areas on each side of the cloaca extending forward somewhat over the sides of the abdomen. The ventral edges of the pectorals are also pale grey. The ventral surface of the tail is light brown except for a whitish patch at the base of the tail.

RAJA JENSENI BIGELOW AND SCHROEDER 1950 — JENSEN'S SKATE

Distribution

Five individuals of *Raja jenseni* have been reported previously from the continental slope off Delaware Bay to Halifax. To these we can add two others taken on the southwest slope of the Grand Bank (Fig. 1, 4–6; Table III). Jensen's skate is a deep-water fish, recorded from 365 to 2295 m. The only individual from less than 640–840 m is the Halifax specimen (No. 1, Table III), recorded from about 365 m, but the recorded location is at a charted depth of over 1460 m. This fish was caught by a vessel presumably longlining for halibut so that the recorded location is probably in error. In halibut fishing, however, on the continental slope the lines may often slip into deeper water than it is intended to fish but most likely not to a depth greater than twice the recorded depth.

Body Proportions and Other Characteristics

Both Grand Bank specimens (No. 6 and 7 of Table III) have median spine and tooth counts similar to those of *R. jenseni* of Bigelow and Schroeder (1927, 1953a, 1954) and the body proportions of Grand Bank specimen No. 6 (Fig. 4, 5; Table III) are generally within the range of or very close to those of Bigelow and Schroeder. Although the *R. jenseni* described by Bigelow and Schroeder (No. 1–5) have no spine in the interspace between the dorsals, our Grand Bank specimen No. 6 possesses a definite median spine in this interspace (Fig. 4). Specimen No. 7 (Fig. 5; Table III) had part of its tail missing, apparently bitten off and healed, but from its body measurements it is presumably larger than specimen No. 1 (850 mm), the largest *R. jenseni* previously recorded. If the length is calculated on the basis of the distance from snout to centre of cloaca (530 mm) being 59.1% of the total length as for the largest female (No. 1), the total length of No. 7 is estimated to be 897 mm; and if this distance is taken to be 57.3% of the total length, as for the next largest specimen (No. 6), the total length is estimated as 925 mm.

The tail posterior to mid-cloaca apparently becomes relatively shorter with increasing total length. Thus many of the other body proportions are a smaller percentage of the total length in the shortest individual, No. 2.

(This statement does not apply to the disc measurements of the second smallest, No. 3, which had an unusually large disc.) In specimen No. 1 caught off Halifax the unusually long interspace between the dorsals and the unusually greater distance from the rear end of the 2nd dorsal base to tip of tail are probably due (judging from the figure of this specimen which is called *Raja granulata* in Bigelow and Schroeder, 1934) to these fins being torn away from the tail at their posterior bases.

Both Grand Bank specimens are grey dorsally and on the ventral surface dark grey with whitish patches in front of and behind the mouth, on the pectorals and pelvics and at the base of the tail (Fig. 5). The general pattern of white areas is balanced left and right especially in specimen No. 7 where the pattern is very similar to that of the closely related *R. hyperborea* shown in Bigelow and Schroeder (1953a, fig. 44 — especially the female) and to that of the *R. hyperborea* in Günther (1887, pl. 4).

Parasites

In the Grand Bank individual (No. 7) there were large numbers of flukes in the stomach. These were identified by Mr S. Prudhoe of the British Museum as *Otodistomum veliporum* (Creplin). A copepod parasite may be seen attached to the cloacal region of the smaller specimen in Fig. 5. Dr Z. Kabata has identified this copepod from a photograph as *Lernaeopoda* sp. The copepod itself was not available for examination.

Food

In the one individual observed, the Grand Bank specimen No. 7, the stomach contents consisted of one well-digested redfish (135 cc).

RAJA LINTEA FRIES 1838

Distribution

Raja lintea has been recorded from southwestern Norway, the Skagerrak, Bohuslan (Sweden), the Faroes, Faroe–Shetland area, Iceland, and West Greenland at depths from 145 to 640 m (Clark, 1930b; Jensen, 1948; Bigelow and Schroeder, 1953a).

In the areas closest to Newfoundland where *R. lintea* is recorded, it has been generally considered to be rare at Iceland where only seven were noted by Saemundsson (1949). However, Saemundsson mentions that he has been informed by Bowman that specimens of this skate taken off the south coast of Iceland are sometimes observed at the Aberdeen market. Also, Rae and Wilson (1955, 1957) obtained four individuals of this species, 65–72 cm long, which were landed in one trip of an Aberdeen longliner from the Loon Deeps, southeast Iceland in September 1954. From West Greenland, Jensen (1914, 1926, 1948) records only 16 specimens, all west of Great Hellefiske Bank, but 13 of these were taken in one otter-trawling set. More recently, Krefft (1960)

has reported the capture of four additional *R. lintea* from West Greenland in 270–287 m at 63°53′N and 63°26′N somewhat southward of Jensen's locations. These included what are probably the largest sizes recorded — two females of 1190 mm total length.

This is a rather warm water species, taken in bottom temperatures from 3.1 to about 6°C. Jensen (1926) obtained 13 individuals of *R. lintea* at a bottom temperature of 3.12°C in a single otter trawl haul on the southern side of the Davis Strait Ridge (66°37′N, 56°37′W, 450 m), but obtained none from a similar set on the cooler northern side of the Ridge (68°08′N, 57°30′W, 400 m) at a bottom temperature of 2.47°C.

The only captures of this skate known to us from the Northwest Atlantic, west and south of West Greenland, are two which we have obtained from the northern slope of the Flemish Cap (Fig. 1, 7–9; Table IV).

Although in our redfish surveys many otter-trawling sets of the *A.T. Cameron* (and also of the *Investigator II* in many areas) have been made at depths from 180 to 730 m off Baffin Island, northern Labrador, and in Ungava Bay (Templeman, 1961) and around the slopes of the continental shelf and deep channels of the whole Canadian offshore area, no *Raja lintea* have been obtained except at Flemish Cap. Nor was *R. lintea* found by Schroeder (1955) in his extensive deep-water investigations extending along the continental slopes of southern Nova Scotia and New England areas nor by the earlier American deep-water investigations (Goode and Bean, 1895). *Raja lintea* is thus likely to be very scarce in the Northwest Atlantic west or south of Greenland except at Flemish Cap unless it lives more deeply here than elsewhere. There seems to be no good reason, however, why this skate should not migrate westward along the southern slope of the Davis Strait Ridge to the Canadian side and very likely it will yet be found on the western side of the Labrador Sea and on the slope of the Northeast Newfoundland Shelf.

There may be a small local population at Flemish Cap possibly derived from the Icelandic area from which an extension of the Reykjanes Ridge less than 2000 m deep extends toward Flemish Cap but is separated from the Cap by about 450 nautical miles of deeper water of 3000 to over 4000 m. No exceptionally deep-water records of *R. lintea* are known to us, the Flemish Cap capture at 730–750 m being apparently the deepest (but we have not seen all the literature relating to the captures in the Scandinavian area). If Flemish Cap has received or receives its *R. lintea* from Iceland, omitting the possibility of a near-bottom migration in the deepest area, we are left with the alternatives of near-bottom migration along Reykjanes Ridge and its southwestward extension and a pelagic swim of about 450 nautical miles to Flemish Cap, or a pelagic swim of twice this distance if the skates followed Reykjanes Ridge to the 1200 m level and then swam pelagically, or almost 3 times this distance if the skates remained near bottom only to the 800 m depth. Near-bottom or mid-water migration should also be possible from Flemish Cap westward to the northern slope of the Grand Bank.

Body Proportions and Other Characteristics

The body proportions, tooth count, and median dorsal spine number of the Flemish Cap specimens are similar enough to those of *R. lintea* recorded from Iceland and Greenland (Table IV) that the species can be identified, but there are some differences. Although the individuals examined in detail from each area are far too few to show the normal range of variation, the two Flemish Cap *R. lintea* examined are narrower in proportion to their length than those examined from Iceland and Greenland. This is seen not only in the greatest width of the disc (Table IV, item 13) (which is subject to considerable variability in successive measurements from the same fish if it is fresh when measured as was Flemish Cap specimen No. 7), but also in width across mid-pupils (item 14), distance between spiracles (item 21), mouth breadth (item 22), and distance between gill slits (items 24, 25). Also, the disc in the Flemish Cap specimens is shorter (item 15) and the tail slightly longer (item 27), although for the latter the Greenland specimen No. 1 is very similar to Flemish Cap specimen No. 7.

In the Flemish Cap specimens (items 30, 31, 32) the median dorsal spines are fewer, 40–42, compared with 45–51 in those from West Greenland and Iceland, the upper-tooth count (50–51) is similar and the lower-tooth count (44–44) is less compared with *R. lintea* from West Greenland and Iceland (47–50/47–50). In the Flemish Cap specimen No. 7 (Fig. 7) the seven median spines on the disc immediately posterior to the two most anterior median spines were counted from scars which are clearly visible. There is so little room between the large basal scars of these spines that it is very unlikely that a larger number was present. In Flemish Cap specimen No. 6, with the smallest number of mid-dorsal spines, all the mid-dorsal spines are clearly visible and no small intermediates are present.

While the upper surface is grey the lower surface of *R. lintea* is more variable in colour, ranging from uniformly white in some adult specimens of *R. lintea* from the Skagerrak (Clark, 1926) to white with a dark spot on each side of the anus and a dark band dissolving posteriorly into spots along the middle of the tail in West Greenland specimens (Jensen, 1948). Others (Bigelow and Schroeder, 1953a, fig. 50, for an Icelandic specimen) may be dark grey along the posterior and lateral borders of the pectorals and pelvics, below the tail and on each side of the cloaca, and have irregular dark markings below the tip of the snout.

When fresh immediately after capture, the upper surface of our Flemish Cap specimen No. 7 was brownish grey and the lower surface (Fig. 8) white except for some darkening on the posterior borders of the pelvics and on the ventral surface of the tail. The edges of the pectorals which are somewhat darkened in the photograph are very thin and had become brown from drying before being photographed but they were originally white to the edges.

Food

Saemundsson (1949) found fish (*Gadus poutassou*) and *Lumpenus lumpretaeformis*) in the stomach of an Icelandic specimen of *R. lintea*. In our specimen No. 6 from Flemish Cap the stomach contents consisted of: *Boreomysis tridens*, 4.5 cc; the pelagic amphipod, *Parathemisto gaudichaudi*, 1 cc; *Pandalus borealis*, 4.5 cc, and a polychaete (sea-mouse type), 0.7 cc. In Flemish Cap specimen No. 7 the stomach contents consisted of shrimp, 26 cc, and scaled lancetfish, *Paralepis* sp. (1), 26 cc.

RAJA MOLLIS BIGELOW AND SCHROEDER 1950

Distribution

Bigelow and Schroeder (1950) described *Raja mollis* from an individual obtained by the *Albatross* in 1883 on the continental slope off southern Nova Scotia. Subsequently, between 1949 and 1953, three additional *R. mollis* were captured in the same general area (Bigelow and Schroeder, 1954; Table V). In our deep-water otter-trawling for redfish, usually at depths to 710–750 m, we have obtained six additional individuals of this species, extending its range greatly to the southwestern Grand Bank and as far northward as off Cape St. David, Baffin Island (Table V; Fig. 1, 10–13). The known range of the species now extends on the North American continental slope from 41°25′N to 64°00′N and in depths from 450–475 to 1570 m. All specimens except one were taken deeper than 710 m. All 10 individuals thus far captured are immature and they range from 195 to 440 mm in length. Because the largest individual of 440 mm, taken on the southwest slope of the Grand Bank, had very immature claspers not extending beyond the tips of the pelvic fins, it is assumed that this species grows considerably larger. It is probable, also, that the mature individuals of the species live deeper than the 710–750-m level which has been the lower limit of our trawling. There would seem to be no good reason why this species should not occur off the southern part of West Greenland. Our most northerly record on the Davis Strait Ridge is approximately half way between Baffin Island and West Greenland.

Body Proportions and Other Characteristics

The body proportions of our *R. mollis* are generally similar to those of the type specimen (Table V), although the tail proportion is slightly longer in the latter.

The tooth-count range of our six *R. mollis* is 54–63/55–64. For the upper jaw this is a slightly wider range but lower average (57.2) than for the earlier four individuals, 54–60 (average 58.5) (Table V). The tooth count may be greater in the larger than in the smaller individuals.

Raja mollis is notable among the skates of the area in having no large spines, but tiny prickles cover the dorsal surface and also the ventral surface of the tail except in the whitened areas near the base and tip of the tail. The

type specimen (Bigelow and Schroeder, 1950, pl. 2) possesses 1 pre-ocular and 1 post-ocular spine on each side, 1 nuchal and 1 scapular spine on each side with a median spine between the 2 scapular spines. In the three specimens subsequently caught by Schroeder, Bigelow and Schroeder (1954) note that the largest individual is different from the type in having two tiny pre-ocular spines and a post-ocular spine behind only one eye.

Our six specimens add to the available information on the variations to be expected in the small spines present from the head to scapular region and on the tail.

They possess from 1 to 4 pre-ocular spines on the left side (1, 2, 2, 2, 4, 4), 1–3 on the right side (1, 2, 2, 3, 3, 3) and 1 on each side post-ocular, except for one individual which has 2 on the left and 1 on the right. Spines are absent in the nuchal area in two, 1 nuchal spine is present in three individuals and 2 in one individual. Two scapular spines (1 left and 1 right) are present in each fish and also a median spine between the 2 scapular spines, but the median spine while small is usually considerably larger than the left or right scapular spines.

Very small median dorsal spines (Fig. 12) are present in the caudal region from near the posterior end of the pelvics to within 1½–2 cm of the anterior base of the 1st dorsal fin in our smallest two specimens but further forward in larger individuals. With a hand lens about 25 of these tiny spines can be recognized in the smallest two individuals but smaller numbers in the larger specimens in which the mid-dorsal spines near the anterior part of the row are larger and distinctly visible. In the larger individuals stronger spines with a backward hook are found along the lateral edges of the tail but these are barely if at all developed on the smallest individual and little developed on the second smallest.

Bigelow and Schroeder (1950) describe the upper surface of the type specimen of *R. mollis* as light greyish (after almost 70 years in alcohol) and the lower surface as pale yellowish without markings. In describing the three additional individuals caught by Schroeder (Bigelow and Schroeder, 1954) the differences between these specimens and the type specimen are discussed but no mention is made of colour.

In our six individuals of this species the dorsal surface is grey or grey with a brownish tinge, and somewhat but not very translucent on each side of the rostral ridge. On the ventral surface of each there are large numbers of darkish grey spots on the posterior half of the pectorals especially near the posterior edges where in some cases the spots are often so close together as to form a darkish fringe. There are smaller spots or darker areas below the snout and occasional spots elsewhere over the ventral surface.

The lower surface of the tail in all six specimens possesses the same grey or brownish grey colour as the dorsal surface but with a white patch at the base of the tail extending in the six specimens backward 0.7–2.3 cm from the posterior axis of the pelvics. There is some white colour ventrally near the tip of the tail and extending forward along the ventral edges of the tail to or

slightly in front of the anterior base of the first dorsal. Also, there is usually but not always a narrow white longitudinal streak devoid of prickles or with prickles considerably reduced along part or most of the mid-ventral line of the tail.

At my request Mr W. C. Schroeder recently checked the colour of the 2 *Cap'n Bill II* specimens (No. 3 and 4 of Table V). He reports (personal communication, July 3, 1964) that in No. 4 (298 mm) on the ventral surface the disc is whitish with a few very small pale greyish spots on the posterior part. Also, a number of such spots, a trifle larger, are scattered on the posterior lobe of the pelvics, with a greyish blotch on the end of each anterior pelvic lobe. The ventral surface of the tail, apart from the white patch at the base of the tail and around its tip, is of the same greyish colour and densely prickled appearance as the upper surface of the disc and tail. For No. 3 (267 mm) on the ventral surface the disc is plain whitish with no small spots anywhere. The posterior lobe of the pelvics has only one or two very small greyish spots and the anterior lobe greyish markings near the tip. The ventral surface of the tail is similar to that in No. 4 above. The upper surface is plain greyish and with a brownish tinge everywhere including pelvics and tail. The colour, therefore, of the recent *R. mollis* specimens of Bigelow and Schroeder (1954) is generally similar to that in our specimens.

In the type specimen, which was preserved in alcohol for almost 70 years before it was described, the rostral cartilage is soft and this softness was thus included as a diagnostic characteristic of the species (Bigelow and Schroeder, 1950). The larger two of Schroeder's more recent specimens were similar in this respect but the smallest (195 mm) had a rather stiff rostral cartilage (Bigelow and Schroeder, 1954). The rostral cartilage of our six specimens is moderately but not very stiff.

Food

There is no published information available on the food of *R. mollis*. All five (all except No. 6) of our *R. mollis* examined contained food (0.5–1.5 cc). All food consisted of crustacea, the total food consisting of the following (cc): shrimp, 2.6 (*Sabinea sarsi*, 2.5); euphausiids, 1.7; mysids, 0.95; hyperiid amphipods, *Parathemisto* type, 0.3; isopod, 0.05; and calanoid copepods 0.1. The various food groups were represented in the following numbers of stomachs (out of 5): shrimp, 3; euphausiids, 4; mysids, 4; amphipods, 2; isopods, 1; and copepods, 1.

ACKNOWLEDGMENTS

The author is grateful to Messrs V. M. Hodder, A. M. Fleming, E. J. Sandeman, and S. J. Olsen who collected some of the material for this paper, to Mr W. C. Schroeder for checking *Raja erinacea* and for additional information on previous records, especially of *Raja mollis*, to Dr W. B. Scott for calling our attention to one of the specimens of *Raja lintea*, to Dr H. J. Squires

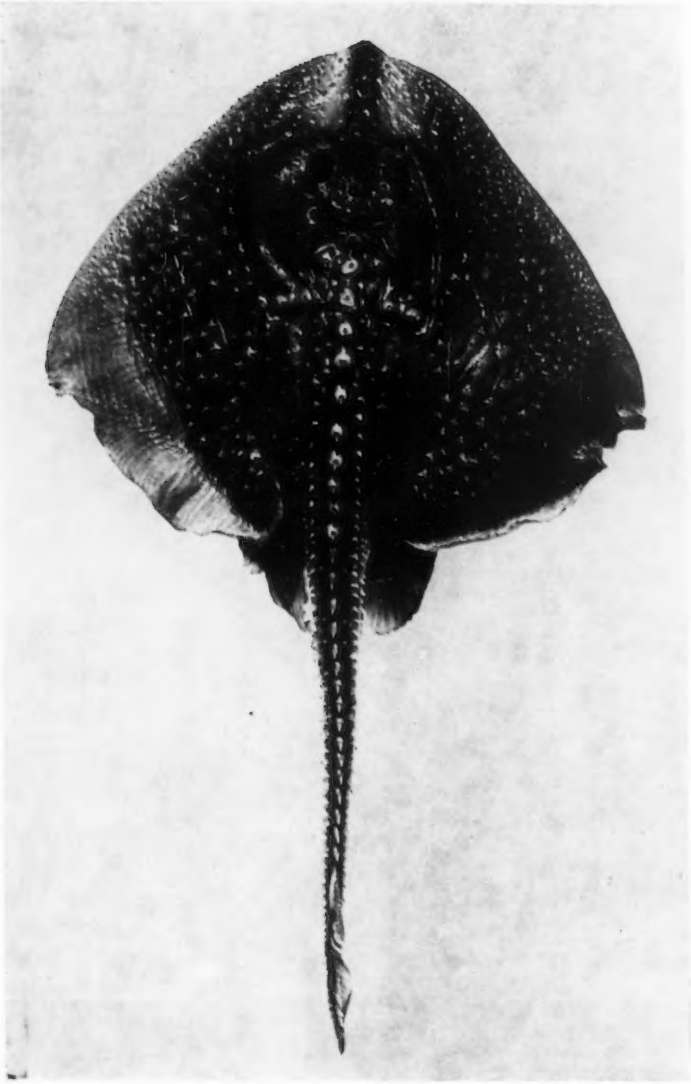


FIG. 2. Dorsal view of *Raja erinacea*, 201 mm, male immature, from Bristol's Hope Cove, Conception Bay, Newfoundland, September 29, 1960.

FIG. 3. Dorsal view of *Raja hyperborea*, 145 mm, female immature, from east of Cape Dyer, Baffin Island, August 24, 1959 (Table II, No. 4).

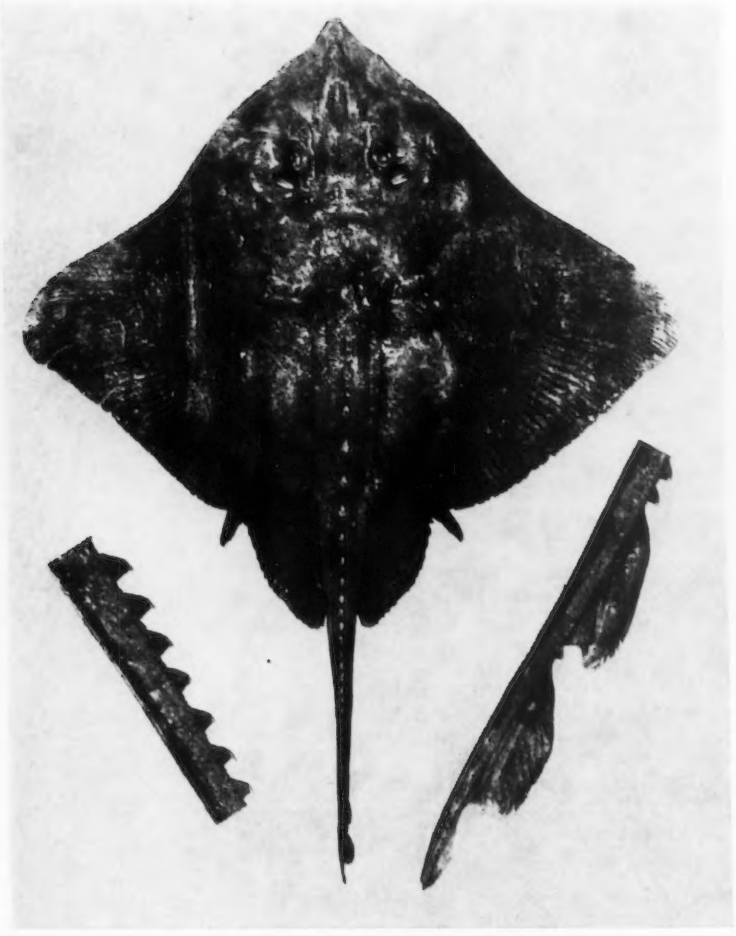


FIG. 4. Dorsal view of *Raja jenseni*, 712 mm, female immature, from southwest slope of the Grand Bank, May 2, 1959 (Table III, No. 6) and a lateral view of the posterior part of the tail of this specimen showing the 9 most posterior median-dorsal spines in front of the 1st dorsal and the median spine in interspace between dorsals.

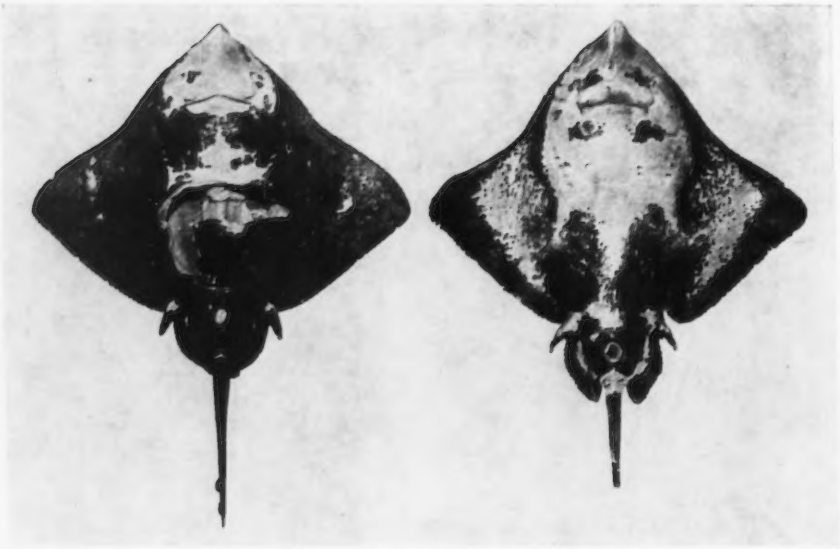


FIG. 5. Ventral view of 2 *Raja jenseni* from southwest slope of the Grand Bank: left, the specimen in Fig. 4; right ,757+ mm, female mature, July 20, 1963 (Table III, No. 7).

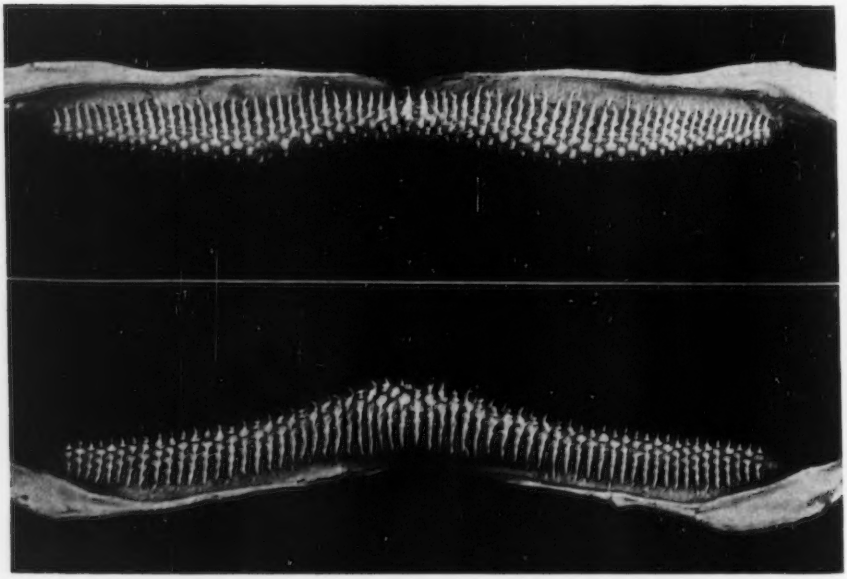


FIG. 6. Upper (above) and lower (below) teeth (natural size) of *Raja jenseni*, 757+ mm, female mature (Table III, No. 7) from internal or dorsal view.

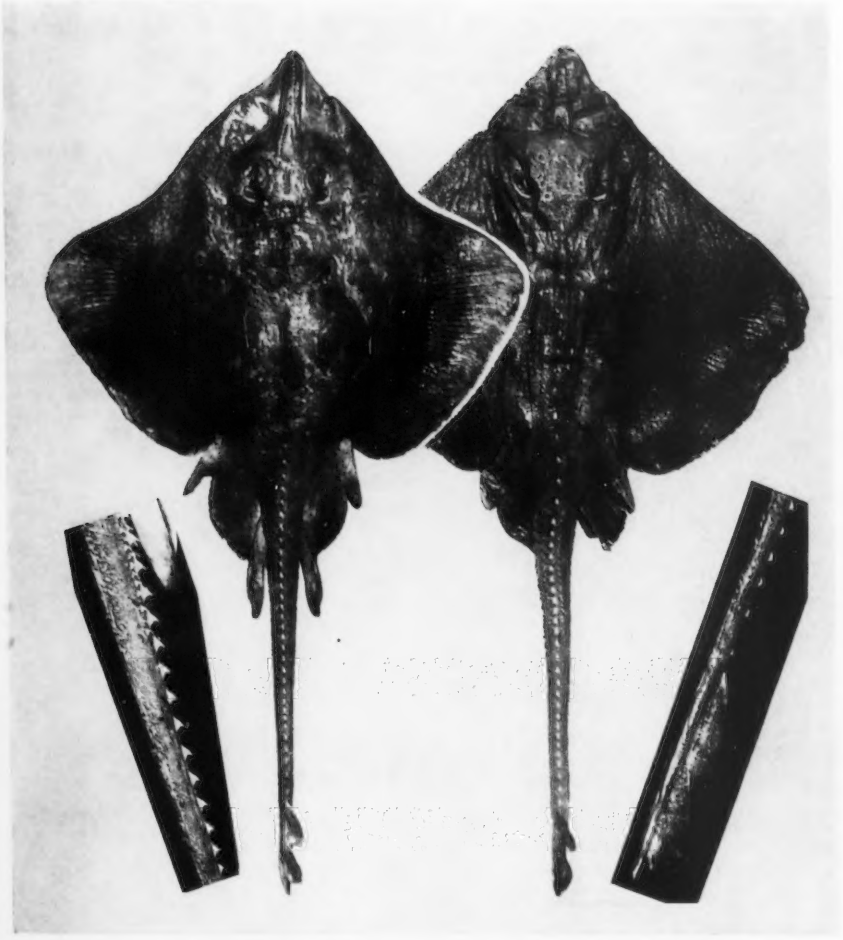


FIG. 7. Dorsal view of 2 *Raja lintea* from northern slope of Flemish Cap: left, 731 mm, male immature but close to sexual maturity, caught on March 21, 1961 (Table IV, No. 7); right, 590 mm, male immature, captured on November 13, 1958 (Table IV, No. 6). Also a lateral view of the posterior part of tail of No. 7 to show median dorsal spines.

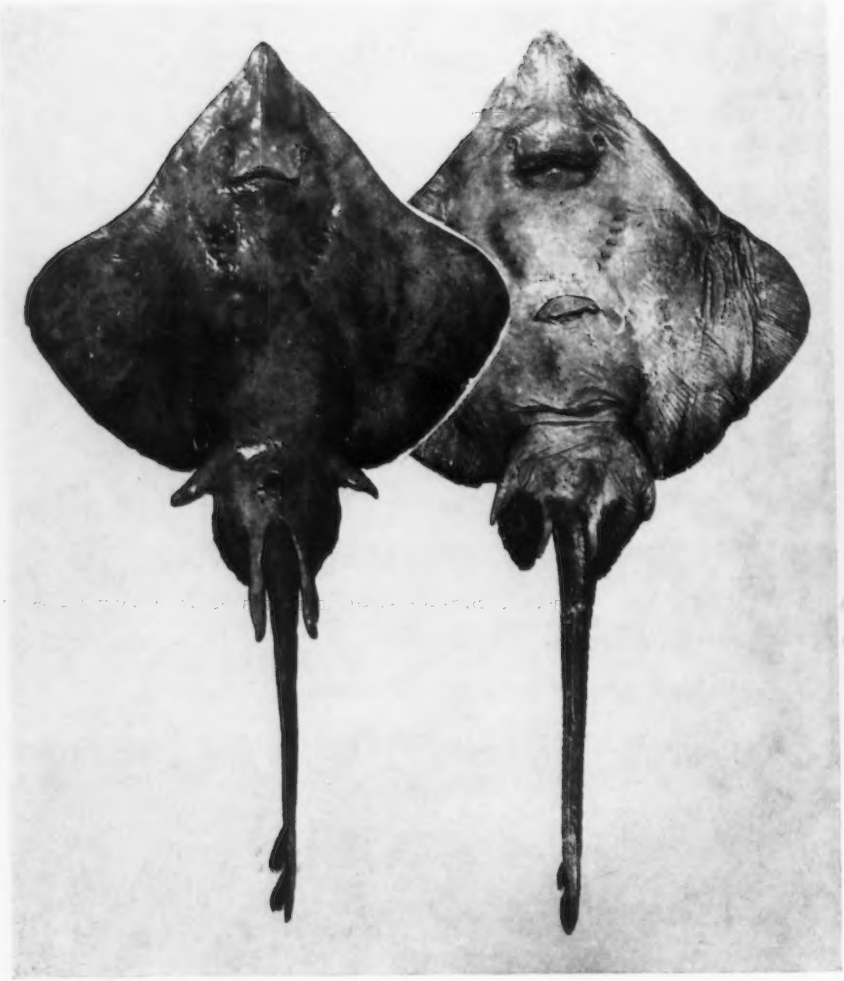


FIG. 8. Ventral view of the 2 *Raja lintea* of Fig. 7: left, No. 7 and right, No. 6 of Table IV.

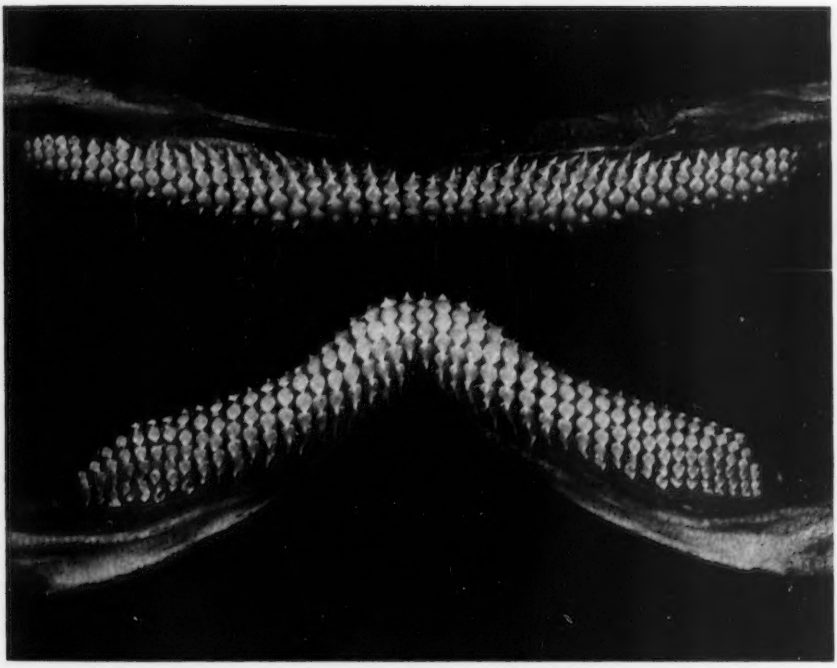


FIG. 9. Upper (above) and lower (below) teeth (×2.2) of *Raja lintea*, 731 mm, male immature (Table IV, No. 7) from internal or dorsal view.

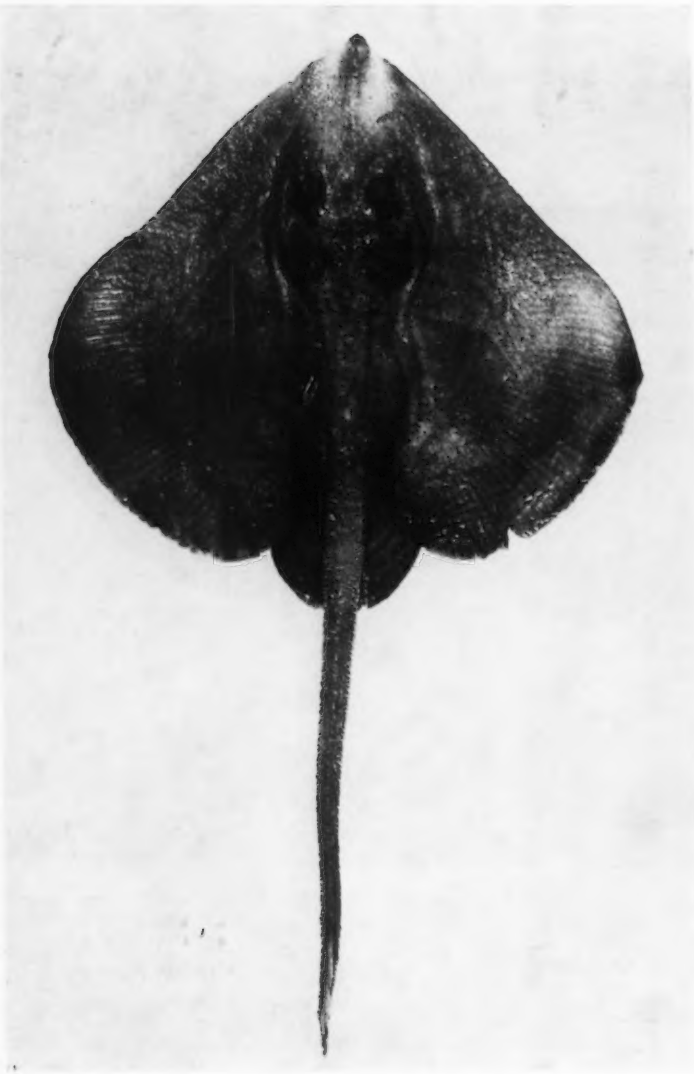


FIG. 10. Dorsal view of *Raja mollis*, 376 mm, male immature, from east of Frobisher Bay, Baffin Island, August 30, 1959 (Table V, No. 10).

Templeman — J. Fish. Res. Bd. Canada

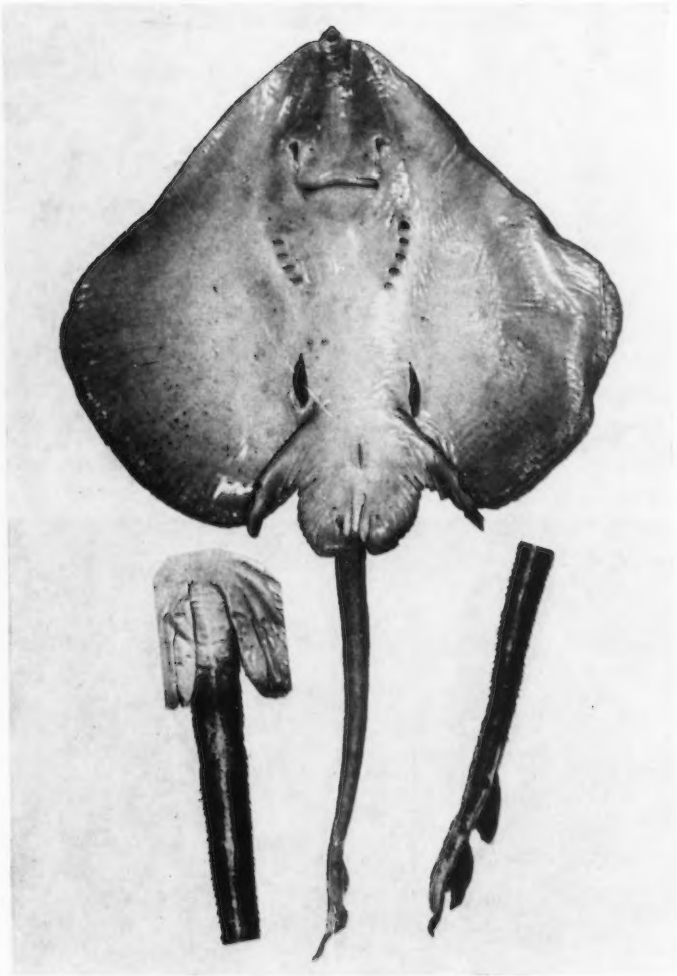


FIG. 11. Ventral view of *Raja mollis*, 297 mm, male immature, from off Cape St. David, Baffin Island, August 28, 1959 (Table V, No. 6) and ventral view of tail of *R. mollis*, 438 mm, male immature, from southwest slope of the Grand Bank, May 5, 1959 (Table V, No. 9).

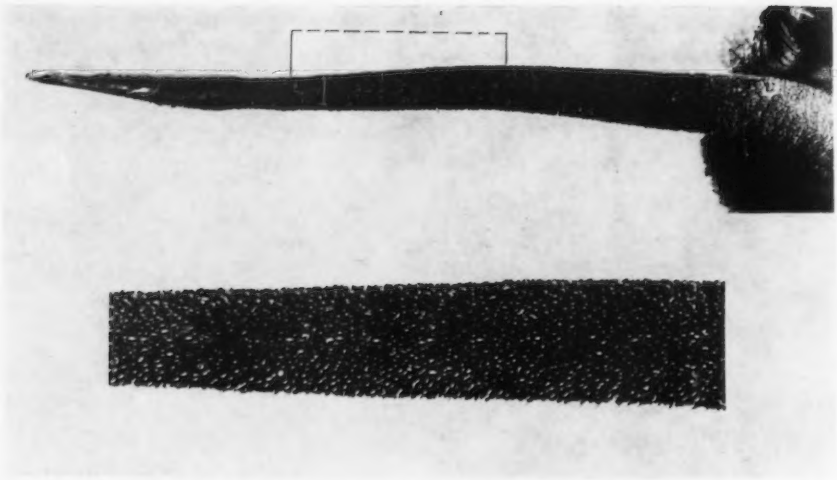


FIG. 12. Above, dorsal view of tail (× 1.0) of *Raja mollis*, 243 mm (Table V, No. 5), and below, more enlarged view of part of tail (× 2.9), to show tiny mid-dorsal spines. (The mid-dorsal spines bend backward, and, although very small, are larger than the neighbouring spines. Their larger white tips are noticeable.)

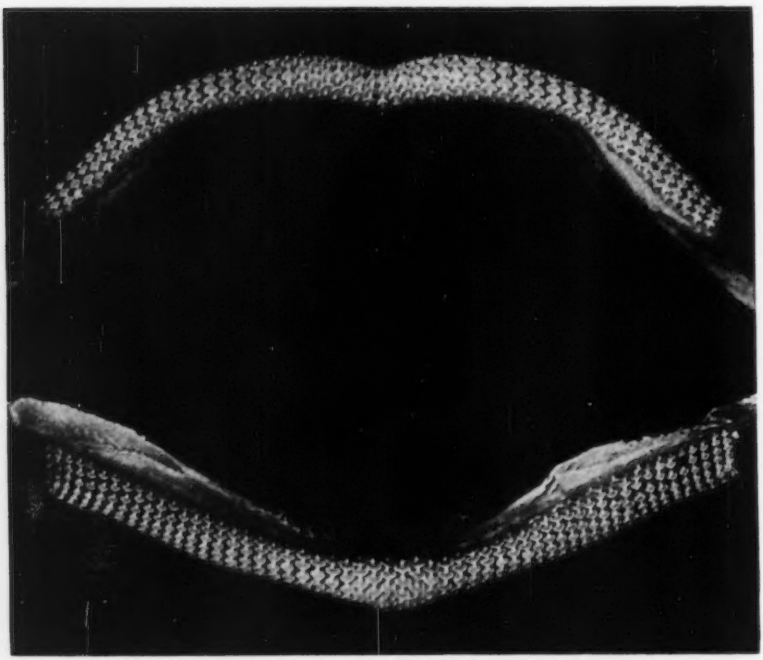


FIG. 13. Upper (above) and lower (below) teeth (× 4.1) of *Raja mollis*, 376 mm, male immature (Table V, No. 10) from internal or dorsal view.

and Mr E.I.S. Rees for assistance in identifying skate food, to Mr S. Prudhoe of the British Museum for identification of fluke parasites of *Raja jenseni* and Dr Z. Kabata for generic identification of a copepod parasite of this skate, to Dr L. P. Schultz for information on dates of capture of *R. jenseni*, and to Dr E. H. Grainger for advice on amphipod nomenclature. Mr E. L. Rowe was responsible for the photography.

REFERENCES

BIGELOW, HENRY B., AND WILLIAM C. SCHROEDER. 1927. Notes on Northwest Atlantic sharks and skates. *Bull. Mus. Comp. Zool. Harvard College*, **68**(5): 239–251.

1934. Chordata, Elasmobranchii. *Biol. Bd. Canada, Canadian Atlantic Fauna*, No. 12(12e), pp. 1–38.

1950. New and little known cartilaginous fishes from the Atlantic. *Bull. Mus. Comp. Zool. Harvard College*, **103**(7): 385–408.

1953a. Fishes of the western North Atlantic. Sawfishes, guitarfishes, skates, rays and chimaeroids. *Mem. Sears Found. Mar. Res.*, **1**(2): 1–588.

1953b. Fishes of the Gulf of Maine. *Bull. U.S. Fish and Wildlife Serv., Fish.*, **53**(74): 1–577.

1954. Deep water elasmobranchs and chimaeroids from the northwestern Atlantic slope. *Bull. Mus. Comp. Zool. Harvard College*, **112**(2): 37–87.

CLARK, R. S. 1926. Rays and skates. A revision of the European species. *Fish. Bd. Scotland*, 1926, No. 1, pp. 1–66.

1930a. *Raja hyperborea*. *Conseil Expl. Mer, Faune Ichthyol. Atlantique Nord*, Species No. 45.

1930b. *Raja lintea*. *Ibid.*, Species No. 52.

GOODE, GEORGE BROWN, AND TARLETON H. BEAN. 1895. Deep-sea and pelagic fishes of the world. *Special Bull. U.S. Nat. Mus.*, No. 2, pp. 1–553 (+ atlas of 417 fig.).

GÜNTHER, ALBERT. 1887. Report on the deep-sea fishes collected by H.M.S. Challenger during the years 1873–1876. *Challenger Rep.*, **22**(Zoology): 1–268.

HUNTSMAN, A. G. 1922. The fishes of the Bay of Fundy. *Contrib. Canadian Biol.*, 1921, No. 3, pp. 49–72.

JENSEN, AD. S. 1914. The selachians of Greenland. *Mindeskr. Jap. Steenstrup Føds, København*, 2, No. 30, pp. 1–40.

1926. Investigations of the Dana in West Greenland waters, 1925. *Conseil Expl. Mer, Rapp. Procès-Verbaux*, **39**: 86–102.

1948. Contributions to the ichthyofauna of Greenland 8–24. *Spolia Zool. Mus. Hauniensis, Skrift. Univ. Zool. Mus. København*, **9**: 1–182.

KOEFOED, EINAR. 1927. Fishes of the sea-bottom. *Rep. Sci. Res. Michael Sars North Atlantic Deep-sea Exped.* 1910, pp. 1–148.

KREFFT, G. 1960. Rare fish. A. Records of the Institut für Seefischerei, Hamburg. *Conseil Expl. Mer, Ann. Biol.*, **15**: 70–72.

LÜTKEN, CHR. 1899. The ichthyological results of the expeditions of the Ingolf. *The Danish Ingolf-Expedition*, **2**(1): 1–39.

RAE, B. B., AND E. WILSON. 1955. Rare and exotic fishes recorded in Scotland during 1954. *Scottish Nat.*, **68**: 23–38.

1957. Rare fishes from distant northern seas. Scotland, 1954. *Conseil Expl. Mer, Ann. Biol.*, **12**: p. 55.

SAEMUNDSSON, BJARNI. 1949. Marine Pisces. *Zoology of Iceland*, **4**(72): 1–150.

SCHROEDER, WILLIAM C. 1955. Report on the results of exploratory otter-trawling along the continental shelf and slope between Nova Scotia and Virginia during the summers of 1952 and 1953. *Deep Sea Research*, Suppl. to Vol. **3**: 358–372.

TEMPLEMAN, WILFRED. 1961. Redfish distribution off Baffin Island, northern Labrador, and in Ungava Bay in August–September 1959. *Rapp. Procès-Verbaux*, **150**: 157–162. [*Also in* Int. Comm. NW Atlantic Fish., Spec. Pub. No. 3, pp. 157–162].

THIELEMANN, M. 1922. Die Fische. *Wiss. Meeresuntersuch., Abt. Helgoland*, N.F. 13, (2), p. 103.

VLADYKOV, V. D., AND R. A. MCKENZIE. 1935. The marine fishes of Nova Scotia. *Proc. Nova Scotian Inst. Sci.*, **19**(1): 17–113.

Tables I–V follow.

TABLE I. Records of the Arctic skate, *Raja hyperborea*, from the western North Atlantic west of West Greenland.

Spec. No.	Year	Date	Locality	Lat N	Long W	Depth *m*	Bottom temp. °C	Length (*mm*) and sex	Observer or reporter and remarks
1	1928	Aug. 8	Smith Sound (position of capture intermediate between West Greenland and Ellesmere Island)	78°14′	74°10′	672	−1.29	200♀	Jensen (1948). Taken in Godthaab Expedition, 1928
2	1928	Aug. 8	" "	"	"	"	"	220♂	" "
3–6	1928	Aug. 17	Jones Sound	75°54′	81°01′	610	−0.59	4♂♂ 240–490	" "
7–13	1928	Aug. 17	" "	"	"	"	"	7♀♀ 260–450	" "
14	1928	Aug. 22	Off Lancaster Sound	74°12′	77°00′	680	−0.38	420♀	" "
15	1928	Sept. 13	E of Baffin Island	67°48′	60°48′	1600	−0.39	440♂	" "
16	1928	Sept. 13	" "	"	"	"	"	290♂	" "
17	1959	Aug. 24	Off Cape Dyer, Baffin Island	66°48′	60°10′	550	1.16	157♀ Immature	Author (research vessel *A.T. Cameron*)

TABLE II. Comparison of body proportions and other characteristics of *Raja hyperborea* from the Canadian area with other similar data on this species. (All percentages are of the total length. No. 4A is the same as No. 4 but with length measurements reduced by calculating the tail posterior to posterior base of 2nd dorsal to be 2.5% of total length. No. 4B is the same specimen as No. 4 but measured fresh at sea immediately after capture.)

Specimen No.:	1	2	3	4	4A	4B
1. Year of capture	...	...	1910	1959	1959	1959
2. Locality of capture	Ivigtut Fjord, SW Greenland		NE Atlantic	East of Cape Dyer, Baffin Island		
3. Position of capture, *lat N*	Ca. 61°	Ca. 61°	60°57′	66°48′	...	...
4. Position of capture, *long W*	...	...	4°38′	60°10′	...	...
5. Depth of capture, *m*	...	...	1098	550	...	...
6. Reference	Bigelow and Schroeder (1953a)		Koefoed (1927)	Author	Author	Author
7. Total length, *mm*	810	850	178[a]	145	136	157
8. Sex	F	M	M	F	F	F
9. Stage of sexual maturity	...	Mature	Immature	Immature	Immature	Immature
10. Disc: extreme width, %	76.5	75.0	71.3	71.7	76.5	72.0
11. Disc: width across mid-pupils, %	...	...	27.5	31.0	33.1	31.8
12. Disc: length, %	55.6	54.3	47.2	49.7	52.9	49.7
13. Snout: length in front of orbits, %	14.3	13.5	10.7	13.1	14.0	...
14. Snout: length in front of mouth, %	13.1	14.6	12.9	13.8	14.7	...
15. Orbits: horizontal diameter, %	3.1	3.0	...	4.2	4.6	...
16. Orbits: distance between, %	6.0	6.5	5.6	7.2	7.7	...
17. Spiracles: length, %	2.3	2.8	...	1.8	1.9	...
18. Spiracles: distance between, %	10.1	10.1	...	10.5	11.2	...
19. Mouth: breadth, %	12.5	12.3	9.8	10.8	11.5	...
20. Nostrils: distance between inner ends, %	10.4	11.0	...	10.8	11.5	...
21. [Gill slits: distance between inner ends] 1st pair, %	19.7	18.8	...	17.9	19.1	...
22. [Gill slits: distance between inner ends] 5th pair, %	13.8	13.6	...	13.8	14.7	...
23. Tip of snout to centre of cloaca, %	57.5	57.1	44.9	47.6	50.7	...
24. Centre of cloaca to tip of tail, %	42.5	42.9	55.1	52.4	49.3	53.5
25. Rear end of 2nd dorsal base to tip of tail, %	2.8	2.2	...	8.4	2.5	8.9
26. Interspace between 1st and 2nd dorsals, %	0.9	1.4	...	0	0	0
27. Large median spines on disc and tail in front of 1st dorsal, *No.*	...	...	...	24	...	...
28. Rows of teeth: upper jaw, *No.*	...	...	...	33	...	...
29. Rows of teeth: lower jaw, *No.*	...	...	...	34	...	...
30. Condition when measured	...	...	...	Out of 10% formalin. In water 2 days	...	Fresh at sea

[a]Koefoed does not give the length in millimetres but in centimetres (18 cm). The other measurements are given in millimetres. The total length of 178 mm represents the sum of the distances from the snout to the centre of the cloaca and from the centre of the cloaca to the tip of the tail.

TABLE III. Comparisons of body proportions and other characteristics of *Raja jenseni* from the Newfoundland area with those of all other known individuals of this species. (All percentages are of the total length. Figures in parentheses for No. 7 are actual measurements in millimetres.)

	Specimen No.:	1	2	3 (Type specimen)	4	5	6	7
1.	Year of capture	1879	1883	1884	1952	1953	1959	1963
2.	Date of capture	Sept. 3	Sept. 4	Aug. 21	July 28	June 27	May 2	July 20
3.	Captured by: Vessel	*Augusta H. Johnston*	*Albatross*	*Albatross*	*Cap'n Bill II*	*Cap'n Bill II*	*A. T. Cameron*	*A. T. Cameron*
4.	" " : Gear	Longline	Bottom trawl	Bottom trawl	Otter trawl	Otter trawl	Otter trawl	Otter trawl
5.	Scientist-in-charge	...	...	...	W. C. Schroeder	W. C. Schroeder	V. M. Hodder	V. M. Hodder
6.	Locality of capture	Continental slope off Halifax	E slope Georges Bank	Continental slope off S New England	Slope of Brown's Bank	Off Delaware Bay	SW slope Grand Bank	SW slope Grand Bank
7.	Position of capture, *lat N*	Ca. 42°37′	41°09′40″	39°34′45″	42°19′	38°47′	44°18′	43°15′45″
8.	" " " , *long W*	Ca. 62°55′	66°02′20″	71°21′30″	64°59′	72°54′	53°22′30″	51°41′15″
9.	Depth of capture, *m*	365	2295	1975	710–800	1070–1090	750–800	640–840
10.	Bottom temperature, *°C*	...	...	...	...	4.18	3.99	...
11.	Reference	Bigelow and Schroeder (1927, 1934) *R. granulata*, 1950, 1953a, 1954	Bigelow and Schroeder (1950, 1953a)		Bigelow and Schroeder (1954)		Author	Author
12.	Total length, *mm*	850	223	541	625	695	712	757+[b]
13.	Weight, *kg*	...	...	...	...	...	...	5.2[c]
14.	Sex	Female	Male	Female	Female	Female	Female	Female
15.	Diameter of largest egg in ovary, *mm*	...	...	...	...	...	5	35
16.	Weight of 2 shell glands, *g*	...	...	...	...	...	1.2	59
17.	Stage of sexual maturity	...	Immature	...	...	...	Immature	Mature
18.	Disc: extreme width, %	77.1	70.2	81.3	...	...	78.5	(637)
19.	Disc: width across mid-pupils, %	31.8	...	...	...	...	35.1	(275)
20.	Disc: length, %	56.5	53.7	60.0	...	...	58.0	(498)

21.	Snout: length in front of orbits, %	15.5	14.4	15.5	...	...	15.7	(141)
22.	Snout: length in front of mouth, %	...	16.9	16.3	...	...	...	...
23.	Orbits: horizontal diameter, %	...	4.4	4.8	...	...	4.1	(38)
24.	Orbits: distance between, %	...	6.2	6.6	...	...	7.3	(59)
25.	Spiracles: length, %	...	2.5	2.8	...	...	2.6	(21)
26.	Spiracles: distance between, %	11.2	10.6	12.0	...	...	11.2	(98)
27.	Mouth: breadth, %	15.8	12.5	12.5	...	...	13.9	(122)
28.	Nostrils: distance between inner ends, %	...	12.8	...	...	...	13.3	(110)
29.	Gill slits: distance between inner ends — 1st pair, %	20.5	18.9	21.6	...	...	22.8	(196)
30.	Gill slits: distance between inner ends — 5th pair, %	13.8	14.0	18.1	...	...	17.4	(143)
31.	Tip of snout to centre of cloaca, %	59.1[a]	51.5	52.8	...	...	57.3	(530)
32.	Centre of cloaca to tip of tail, %	40.9[a]	48.5	47.2	...	...	42.7	...
33.	Rear end of 2nd dorsal base to tip of tail, %	5.3	3.9	2.6	...	...	2.7	...
34.	Interspace between 1st and 2nd dorsals, %	3.4	0.8	0.9	...	...	0.7	...
35.	Large median spines on disc anterior to axils of pectorals, *No.*	...	8	7	8	6+ ? 3 or 4	8	7
36.	Large median spines on disc and tail anterior to 1st dorsal, *No.*	...	31	24–25	29	26+ ? 3 or 4	30	22+[d]
37.	Rows of teeth: upper jaw, *No.*	56	...	66	60	51	62	67
38.	Rows of teeth: lower jaw, *No.*	56	...	...	...	...	61	61
39.	Condition when measured	...	...	...	...	...	Preserved 10% formalin and soaked in water 1 day	Fresh. Thawed in water after freezing

[a]Assuming cloaca to be 30 mm long as in No. 7.
[b]The end of the tail of this specimen was absent, probably bitten off.
[c]Weight whole fresh.
[d]This specimen had probably at least 6 or 7 median spines missing with the lost portion of the tail.

TABLE IV. Comparison of body proportions and other characteristics of the Flemish Cap *Raja lintea* in relation to those of other *R. lintea* of the Icelandic and West Greenland areas. (All percentages are of the total length.)

	Specimen No.:	1	2	3	4	5	6	7
1.	Locality of capture	W Greenland	W Greenland	W Greenland	Iceland	Iceland	N Slope Flemish Cap	N Slope Flemish Cap
2.	Position of capture, *lat N*	66°35′	66°45′	66°53′	...	...	47°56′	48°22′
3.	" " " , *long W*	56°38′	56°39′	56°17′	...	...	46°23′	44°45′
4.	Depth of capture, *m*	580	370–440	385–410	...	...	730–750	635–640
5.	Bottom temperature, °*C*	3.9	3.3 to 3.4	3.4	...	...	3.62	3.67
6.	Reference	Lütken (1899)[a] Jensen (1948)	Jensen (1948)	Jensen (1948)	Bigelow and Schroeder (1953)[a]		Author	Author
7.	Total length, *mm*	662	1080	810	970	1050	590[d]	731
8.	Weight, *kg*	...	...	...	...	...	...	1.8
9.	Sex	Male	Male	Female	Male	Female	Male	Male
10.	Distance posterior tip pelvic fin to tip of clasper, *mm*	...	...	...	...	...	−12[e]	+47[e]
11.	Longitudinal rows of alar spines, *No.*	...	...	...	3	...	0	1+
12.	Stage of sexual maturity	Immature	...	...	Mature	...	Immature	Immature but close to sexual maturity
13.	Disc: extreme width, %	64.5	...	...	65.7	64.0	60.2	59.4
14.	Disc: width across mid-pupils, %	33.8	...	...	...	...	29.3	29.1
15.	Disc: length, %	...	...	...	54.3	54.3	49.7	47.5
16.	Snout: length in front of orbits, %	...	...	...	14.8	16.5	14.9	14.6
17.	Snout: length in front of mouth, %	18.9	...	...	16.3	18.2	...	15.5
18.	Orbits: horizontal diameter, %	...	...	...	3.6	4.0	3.8	2.7

19.	Orbits: distance between, %	5.0	...	...	5.1	4.1	4.9	4.8
20.	Spiracles: length, %	2.1	...	...	2.6	2.6	1.7	1.9
21.	Spiracles: distance between, %	...	...	...	8.0	8.1	7.1	7.0
22.	Mouth: breadth, %	9.1	...	...	10.4	10.0	...	8.1
23.	Nostrils: distance between inner ends, %	8.6	...	...	8.6	9.3	9.0	8.5
24.	Gill slits: distance between inner ends — 1st pair, %	...	...	...	15.5	15.3	12.8	13.1
25.	Gill slits: distance between inner ends — 5th pair, %	...	...	...	9.7	9.7	8.8	8.6
26.	Tip of snout to centre of cloaca, %	49.8	...	...	51.0	53.2	49.3	49.6
27.	Centre of cloaca to tip of tail, %	50.2[b]	...	...	49.0	46.8	50.7	50.4
28.	Rear end 2nd dorsal base to tip of tail, %	...	...	...	0.5	0.4	1.2	1.5
29.	Interspace between 1st and 2nd dorsals, %	...	...	...	2.0	0	0	0
30.	Large median dorsal spines: total, *No.*	47	48	45	51[c]	...	40	42
31.	Rows of teeth: upper jaw, *No.*	...	49	47	50	50	51	50
32.	Rows of teeth: lower jaw, *No.*	...	50	47	48	48	44	44
33.	Condition when measured	...	...	...	...	...	Preserved in 10% formalin and soaked in water for 1 day	Fresh. Thawed after freezing

[a] *Raja ingolfiana*.
[b] Allowing 5 mm for half length of cloaca.
[c] From Bigelow and Schroeder (1953a, fig. 49).
[d] Total length 620 mm fresh at sea immediately after capture.
[e] Distance from posterior tip of pelvic fin to tip of clasper is negative if the clasper does not extend as far as the tip of the pelvic fin and positive if it extends beyond it.

TABLE V. Comparison of body proportions, and other characteristics of *Raja mollis* from the Newfoundland area with those of all other known individuals of this species. (All percentages are of the total length.)

Specimen No.:	1 (Type)	2	3	4	5	6	7	8	9	10
1. Year of capture	1883	1949	1952	1953	1958	1959	1959	1959	1959	1959
2. Date of capture	Sept. 2	June 19	July 26	July 12	Dec. 2	May 3	May 3	May 5	Aug. 28	Aug. 30
3. Captured by: Vessel	*Albatross*	*Caryn*	*Cap'n Bill II*	*Cap'n Bill II*	*A. T. Cameron*	*A. T. Cameron*	*A. T. Cameron*	*A. T. Cameron*	*A. T. Cameron*	*A. T. Cameron*
4. " " : Gear	...	Otter trawl	Otter trawl	Otter trawl	Otter trawl	Otter trawl	Otter trawl	Otter trawl	Otter trawl	Otter trawl
5. Scientist-in-charge	...	W. C. Schroeder	W. C. Schroeder	W. C. Schroeder	E. J. Sandeman	V. M. Hodder	V. M. Hodder	V. M. Hodder	Author	Author
6. Locality of capture	Continental slope, S of southern Nova Scotia	Continental slope, E of Georges Bank	Continental slope off southern Nova Scotia	Continental slope off southern Nova Scotia	NE Nfld Shelf	SW slope of Grand Bank		SW slope Grand Bank	Off Cape St. David, Baffin I.	E of Frobisher Bay, Baffin I.
7. Position of capture, *lat N*	41°53′	41°25′	42°40′	42°40′	50°53′50″	43°39′	43°39′	43°10′	64°00′	63°01′
8. Position of capture, *long W*	65°35′	65°54′	63°51′	63°52′	50°51′00″	52°20′	52°20′	51°34′	58°10′	60°11″
9. Depth of capture, *m*	1570	760–895	850–880	760–770	715	735–745	735–745	450–475	730	715–730
10. Bottom temperature, °*C*	3.9	...	...	4.3	4.01	3.97	3.97	2.57	3.52	3.57
11. Reference	Bigelow and Schroeder (1950, 1953a)	Bigelow and Schroeder (1954)	Bigelow and Schroeder (1954)	Bigelow and Schroeder (1954)	Author	Author	Author	Author	Author	Author
12. Total length, *mm*	262	Ca. 195	267	298	243	360	291	438(440)	297(302)	376(390)
13. Weight, *g*	...	...	...	...	73	205	102	...	108	226
14. Sex	Male	Male	Male	Male	Male	Female	Female	Male	Male	Male
15. Distance posterior tip pelvic fin to tip of clasper, *mm*	...	...	...	...	–5	...	...	0	–7	–6
16. Longitudinal rows of alar spines, *No.*	0	...	...	...	0	...	...	0	0	0
17. Diameter of largest egg in ovary, *mm*	...	...	...	...	...	1	0.7	...	...	...
18. Weight of 2 shell glands, *g*	...	...	...	...	...	0.1	<0.1	...	...	...
19. Stage of sexual maturity	Immature	Immature	Immature	Immature	Immature	Immature	Immature	Immature	Immature	Immature

20. Disc: extreme width,%	61.0	...	...	...	63.0	65.6	62.5	63.0(61.4)	62.3(61.9)	63.3(63.1)
21. Disc: width across mid-pupils, %	...	...	...	...	42.0	41.7	40.5	38.1(40.0)	39.4(39.7)	36.7(39.5)
22. Disc: length, %	49.7	...	...	...	51.6	54.2	53.3	51.8(51.6)	51.5(51.0)	52.7(53.1)
23. Snout: length in front of orbits, %	14.9	...	...	...	14.8	16.8	15.6	15.3	15.5	14.9
24. Snout: length in front of mouth, %	15.7	...	...	...	16.5	17.8	16.5	15.8	16.5	16.2
25. Orbits: horizontal diameter, %	3.8	...	...	...	4.9	4.2	4.1	4.1	3.8	3.8
26. Orbits: distance between, %	3.8	...	...	...	4.3	3.9	4.1	4.1	4.4	4.3
27. Spiracles: length, %	2.1	...	...	...	2.3	1.9	2.1	1.8	1.7	1.7
28. Spiracles: distance between, %	7.1	...	...	...	7.4	7.2	7.1	7.0	7.1	7.1
29. Mouth: breadth, %	8.0	...	...	...	8.3	8.6	8.3	8.7	9.1	9.2
30. Nostrils: distance between inner ends, %	8.6	...	...	...	8.3	8.3	8.6	8.2	8.4	8.5
31. Gill slits: distance between inner ends — 1st pair, %	13.2	...	...	...	14.4	14.0	13.8	13.2	13.5	13.3
32. Gill slits: distance between inner ends — 5th pair, %	8.8	...	...	...	8.6	8.3	8.4	7.8	8.2	7.7
33. Tip of snout to centre of cloaca, %	42.8	...	...	...	45.3	46.3	45.2	46.6	45.6	45.5
34. Centre of cloaca to tip of tail, %	57.2	...	...	...	54.7	53.7	54.8	53.4(54.3)	54.4(55.0)	54.5(55.4)
35. Rear end of 2nd dorsal base to tip of tail, %	3.4	...	...	...	2.5	4.7	3.8	3.7(3.4)	3.7(3.6)	4.3(4.1)
36. Interspace between 1st and 2nd dorsals, %	0	...	...	...	0	0	0.5	0	0	0
37. Rows of teeth: upper jaw, *No.*	60[a]	54	60	60	55	63	54	62	54	55
38. Rows of teeth: lower jaw, *No.*	...	...	...	...	60	64	55	63	55	57
39. Condition when measured	Out of alcohol	...	...	...	All these specimens were measured after preservation in 10% formalin and soaking in water for 2 days. Measurements in parentheses are from fresh specimens before preservation.					

[a]Bigelow and Schroeder (1954).

Effects of Light on Growth of Oysters, Mussels, and Quahaugs[1]

By J. C. Medcof and C. J. Kerswill

Fisheries Research Board of Canada
Biological Station, St. Andrews, N. B.

ABSTRACT

Rearing experiments with small shellfish were carried out in Bideford River, Prince Edward Island (salinity 28‰) and in Bras d'Or Lake, Nova Scotia (salinity 20‰). Paired lots were grown in light-exposed and shaded compartments of floating trays and in an exposed and a shaded area on an intertidal beach. Shading increased linear shell growth of oysters (*Crassostrea virginica*) and mussels (*Mytilus edulis*) approximately 1½ times but reduced the thickness:length ratio. Quahaug (*Mercenaria mercenaria*) shell growth and shell proportions were unaffected by treatment differences. Light exposure increased plumpness of meats of all species, and in oysters it increased specific gravity, fluting, and pigmentation of shells.

INTRODUCTION

Oysters and other species of inshore sedentary molluscs are commonly cultivated on intertidal beaches or in shallow water. Here they are subject to extreme variations in light but effects of these variations on the molluscs have not been properly examined.

Huntsman (1921) realized this and has stimulated the studies reported here.

EXPERIMENTS

Bideford River Tray Experiments, 1939 and 1940

Kerswill (MS, 1941) carried out his light experiments on oysters, mussels, and quahaugs in Bideford River, Prince Edward Island, where salinities are relatively high (variable around 28‰). He used an industrial oyster rearing tray (Medcof, 1961) but divided the interior by wooden partitions into eight equal compartments (0.9 × 0.6 m). Alternate compartments had wooden covers and the others had covers of "Celloglass", a flexible, transparent plastic reinforced with window screening.

On June 9, 1939, he distributed approximately 100 measured quahaugs among the four compartments at one end of the tray and 50 oysters and 50 mussels (all measured) in the four compartments at the other end. He separated the oysters and mussels in each compartment with a wire cloth partition. Every few days he examined the tray, removed all fouling growths and separated any animals that had become clustered. On September 15, 1939, he counted and remeasured the stocks. He repeated this experiment in Bideford River in 1940 (June 11–September 12) using different numbers of animals of the same species (Table I).

[1]Received for publication August 19, 1964.

J. Fish. Res. Bd. Canada, 22(2), 1965.
Printed in Canada.

TABLE I. Growth records for paired lots of shellfish, shaded and exposed to direct sunlight. The values shown are means and standard errors (L and W mean length and width).

Species and year	Shaded					Exposed				
	No. measured		Size			No. measured		Size		
	Start	End	Start	End	Increase	Start	End	Start	End	Increase
			mm	*mm*	%			*mm*	*mm*	%
Bideford River trays										
			$\frac{L + W}{2}$					$\frac{L + W}{2}$		
Oysters										
1939	50	50	20.4 ± .3	50.5 ± .6	147	50	45	21.4 ± .3	41.3 ± .9	93
1940	10	10	21.3	49.6	133	7	7	22.8	43.8	92
Mussels			Length					Length		
1939	50	45	24.6 ± .3	36.1 ± .4	47	50	44	25.2 ± .3	34.5 ± .5	37
1940	60	45	14.0 ± .6	28.5 ± .1	104	60	49	14.1 ± .1	25.8 ± .3	84
Quahaugs			Length					Length		
1939	95	95	28.5 ± .4	37.3 ± .3	31	97	97	28.5 ± .4	36.3 ± .4	28
1940	145	145	31.3 ± .5	35.1 ± .5	13	131	131	31.4 ± .4	35.9 ± .5	14
Bras d'Or trays										
			$\frac{L + W}{2}$					$\frac{L + W}{2}$		
Oysters										
1939	250	92	37	59	60	250	105	37	52	41
1940	187	187	59	65	10	182	182	55	62	13
Bideford River bottom test										
Oysters			Length					Length		
1943	61	52	48.9	69.7	43	55	55	49.6	63.2	27
Huntsman's experiment (St. Andrews, N.B.)										
Mussels			Length					Length		
1920	20 (ca.)		7.5	14.4	92	20 (ca.)		7.5	9.5	27

In 1939 there was a conspicuous growth of green algae in the lighted compartments but little in the dark. In contrast, there were only scanty settlements of mussel spat in the lighted compartments but heavy sets in the dark. In 1940 there were lighter growths of algae but the mussel sets were about the same as in 1939. The regular cleaning of the tray prevented these fouling growths from clogging the wire-screen bottom (12.7-mm mesh) to a degree that would be expected to seriously affect water circulation.

Bras d'Or Lake Tray Experiments, 1939 and 1940

Medcof carried out tray experiments in Bras d'Or Lake, an area where salinity is low (variable around 20‰), to supplement the Bideford River studies. His tray was similar to Kerswill's except that the compartments were larger (0.9 × 1.2 m), the lighted compartments were covered with window glass instead of "Celloglass", and 6.4-mm mesh was used for the wire-screen bottom (Medcof, MS, 1939).

In June 1939 he placed 250 small oysters in each compartment and moored the tray at Gillis Cove. In September the test animals were counted and random samples were measured. Throughout the experiment the tray and the oysters were cleaned at 2-week intervals. Algal growths were especially luxurious in the lighted compartments and newly-settled mussels were commonest in the dark. In November the tray was sunk in deep water for the winter to prevent ice damage.

In early May 1940 the tray was raised again and the experiment was continued with the same stocks. In November 1940, random samples were again measured. That year the cleaning was less regular and fouling growths sometimes interfered with water circulation and lighting (Medcof, MS, 1940).

Bideford River Intertidal Beach Experiment, 1943

From May 4 to November 2, 1943, Medcof studied effects of light on two lots of oysters set out on the bottom in the intertidal zone on a sandy beach in Bideford River where they were air-exposed 30% of the time (calculated from tide gauge readings). One lot was completely exposed to natural light. The other was shaded by a wooden platform, 1.2 m square, which was fixed 30 cm above beach level (Medcof, MS, 1943).

At the start of the experiment each lot was set in a slab of newly-mixed concrete, 0.6 m square and 6 cm thick. The oysters (64 in each lot) were arranged at 7.5-cm intervals with their hinge ends imbedded 2 mm deep and their lip ends tilted slightly upward. The concrete set in a few hours and held most of the oysters firmly in position throughout the season. Otherwise they would have been quickly dispersed by wave action.

Sometimes sand accumulated about these oysters and mussel and oyster spat settled on them — especially on the shaded animals. There were heavy growths of algae on the unshaded animals. The lots were cleaned every week or 10 days by washing away the sand and removing the algae and mussels but

it was impossible to remove the oyster spat. On November 2 the surviving animals were counted and measured.

OBSERVATIONS

Linear Growth of Shells

Table I summarizes records of mean sizes (lengths or average diameters) of the experimental animals. In some cases only means are shown. In others, standard errors are also listed.

The records for paired lots of oysters show that length growth of shaded lots was roughly 1½ times that of the exposed. This is true for stocks reared both in trays and on the bottom in low- and high-salinity areas. The data for the 1940 Bras d'Or test are discordant and this may be attributed to the poor cleaning of the tray.

Mussels behaved like oysters. The light-exposed animals grew 10–20% less than the shaded. This agrees with Coulthard's (1929) results. Huntsman's results (Table I) for small mussels also agree with ours, but the difference between the growth of shaded and exposed lots was much greater in his experiment.

Quahaug growth showed no between-treatment differences.

Cupping of Shells

The oyster most sought after by connoisseurs is "cupped", i.e. its thickness is great in proportion to its length or average diameter. This ratio is higher for light-exposed than for shaded oysters (Table II). In many of the light-exposed oysters the upper valve was distinctly arched so the animal was convex on both upper and lower sides. The shaded oysters usually had flat or concave upper valves. The paired lots in the 1940 Bras d'Or tray, which was not regularly cleaned, were the only measured stocks that failed to show this between-treatment difference in cupping.

Mussels show the same tendency as oysters. This is not conspicuous for the large animals (24.6 mm) used in the 1939 test, but it shows up in the smaller ones (14.0 mm) used in 1940 (Table II). It is still clearer in the very small animals (7.5 mm) used by Huntsman (1921).

Quahaugs showed no between-treatment difference in cupping.

Roominess of Shells

By "roominess" we mean the volume of the space between the shells expressed as a fraction of the total volume of the whole animal when its shells are tightly closed. We measured this for oysters and quahaugs. Table II shows that, in 3 out of 4 of the paired lots of oysters, roominess was greater for the exposed than for the shaded animals. From previous measurements of larger oysters, roominess seemed to decrease with size (Medcof, MS, 1940), but in the present experiments this effect is not indicated.

Shell shape in quahaugs is less variable than in oysters, and there is no evidence in Table II that their roominess was affected by differences in experimental treatments.

Shell Structure

Oyster shells are composed of heavy, hard, nacreous layers and of light, soft, chalky deposits (Medcof, 1944). The relative amounts of these materials in shells affect their strength and specific gravity. Table II shows that shell specific gravity was higher for light-exposed than for shaded oysters and inspection showed that their shells had fewer chalky deposits.

Table II. Shell characteristics and fatness of meats of paired lots of shellfish grown in shade (S) and exposed (E) to sunlight. Values shown are means and standard errors.

	Cupping		Roominess		Shell structure		Fatness	
	Thickness / Length[a]		*Space between shells / Total vol. of animal*		*Specific gravity*		*Index of condition*	
	Bideford River tray							
Oyster	S	E	S	E	S	E	S	E
1939	0.33	0.37	0.49	0.51	2.28	2.34	73	96
1940	0.27	0.33	–	–	2.22	2.38	68	80
Mussels								
1939	0.37 ±.003	0.37 ±.003	–	–	2.34	–	20	52
1940	0.38 ±.009	0.40 ±.006	–	–	–	–	63	80
Quahaug								
1939	0.54	0.54	0.60	0.61	2.65	2.69	45	59
1940	–	–	0.60	0.59	–	–	51	53
	Bras d'Or tray							
Oyster								
1939	0.334 ±.002	0.344 ±.003	0.48	0.47	1.99	2.14	80	86
1940	0.340 ±.003	0.341 ±.003	0.42	0.43	–	–	88	89
	Bideford River bottom							
Oyster								
1943	–	–	0.45	0.48	2.24	2.28	110	105

[a]Or average diameter.

There was no evidence that shell structure (specific gravity) of quahaugs was affected by differences in treatment. We made no observations on mussels.

Fatness of Meats

Measurements of fatness or plumpness of meats (index of condition) were made on paired samples of our shellfish by the senior author (Table II) following the regular procedure of expressing the dry weight of meats measured in grams × 1000, as a fraction of the volume of the space between the valves measured in millilitres (Medcof and Needler, 1941). The samples from the Bideford River tray experiment were all formalin-preserved and the fatness values are accordingly low (Medcof, MS, 1943). But the samples from the Bras d'Or tray and Bideford River bottom tests were all processed fresh.

The work of Baird and Drinnan (1957) shows the complexity of factors affecting fatness. But our results for paired lots of tray-reared stocks show that fatness was higher in all the light-exposed shellfish (even in quahaugs) than in the shaded. The only exception is the result for the 1943 bottom experiment. For this we can offer no explanation.

Other Characteristics

From general observations, light-exposed oysters seemed more symmetrical and more ornamented than the shaded. They were blunt at the edges (there were no thin lips) and the margins of their lower valves tended to be "fluted". This was most conspicuous in the Bideford River bottom experiment in which one-third of the light-exposed animals were distinctly fluted and consequently toothed on the margins.

The outer surfaces of upper valves of the exposed oysters were often ornamented with coloured radial markings — mostly green. In shaded oysters the upper valves were uniformly brown or mottled green and brown. The quahaugs were white regardless of differences in experimental treatment. No observations were made on our mussels, but Huntsman (1921) and Coulthard (1929) both noted that the new shell deposited by their light-exposed animals was jet black whereas that of mussels grown in the dark was pale brown.

DISCUSSION

Our observations are not sensitive enough to indicate how intense the lighting must be before it begins to exercise depressing effects on linear shell growth, and Coulthard's (1929) are not critical on this point. But there is some evidence that it need not be very strong. Huntsman (1921) reared mussels in complete darkness and found that their growth was nearly four times as great as that of light-exposed animals. In contrast, the wood-covered compartments of trays we used in 1939 and 1940 were probably dimly lit during the day by light reflected from the bottom or scattered by suspended matter in the water. This low illumination could account for the much smaller advantage

(average 15%) which shading seems to have provided the mussels in our tray tests as compared with Huntsman's (65%).

A different explanation for this disparity postulates that growth sensitivity to light decreases with increase in size of shellfish and argues that Huntsman got a great difference between his paired lots because his mussels were very small. Our own experiments involved stocks showing considerable differences in initial size (Table III), but within these limits there is no support for the theory that growth sensitivity to light decreases with size.

It appears from our experiments that shell growth and shell proportions of the quahaug, which is a burrowing species, are little affected by light. It might be argued, as Belding (1912) has suggested, that this animal behaves atypically in trays. Nevertheless, from Kerswill's observations (1949), it seems that tray growth in 1939 and 1940 was not very different from that of quahaugs in their natural habitat. This being the case, we may conclude that they are indeed insensitive to light effects on shell growth.

Even in quahaugs, light exposure increased meat yield (index of condition) in spite of the fact that shell growth seemed unaffected. Thus, all our results on fatness agree in suggesting that, although light may retard linear growth of shells, it may not affect growth of soft parts. The mantle edge is the shell-secreting organ, and in oysters and mussels light seems to reduce its ability for marginal shell production but to increase its ability to produce pigments.

TABLE III. Comparison of initial mean sizes of paired lots of mussels and oysters and the relative growths of shaded and exposed lots. (The data for the 1940 Bras d'Or experiment are omitted because the tray was not regularly cleaned.)

Year	Initial size	Length increase		$\frac{\text{Increase of shaded}}{\text{Increase of exposed}}$
		Shaded	Exposed	
	mm	*mm*	*mm*	%
		Mussels		
1920	7.5	6.9	2.0	340
1940	14	14.5	11.7	124
1939	25	12.5	9.3	134
		Oysters		
1939	20–21	30.1	19.9	151
1940	21–23	28.3	21.0	134
1939	37	22.0	15.0	147
1943	49–50	20.8	13.6	153

Mussel and oyster culturists could make use of the findings of our simple experiments to improve their products. But to take full advantage of the effects of light, more penetrating experiments are needed to define its action in the environment and in the physiology of these animals.

REFERENCES

BAIRD, R. H., AND R. E. DRINNAN. 1957. The ratio of shell to meat in *Mytilus* as a function of tidal exposure to air. *J. Cons. Expl. Mer*, **32**(3): 329–336.

BELDING, D. L. 1912. A report upon the quahaug and oyster fisheries of Massachusetts. Commonwealth of Mass., Boston, 112 pp.

COULTHARD, H. S. 1929. Growth of the sea mussel. *Contrib. Canadian Biol. Fisheries*, **4**: 123–136.

HUNTSMAN, A. G. 1921. The effect of light on growth in the mussel. *Trans. Roy. Soc. Canada*, **15**: 23–28.

KERSWILL, C. J. MS, 1941. Some environmental factors limiting growth and distribution of the quahaug, *Venus mercenaria* L. *Fish. Res. Bd. Canada, MS Rept. Biol. Sta.*, No. 187, 104 pp.

1949. Effects of water circulation on the growth of quahaugs. *J. Fish. Res. Bd. Canada*, **7**(9): 545–551.

MEDCOF, J. C. MS, 1939. Oyster investigations in the Bras d'Or Lake and studies on the condition factor of oysters. *Fish. Res. Bd. Canada, MS Rept. Biol. Sta.*, No. 162, 92 pp.

MS, 1940. Oyster investigations in 1940. *Ibid.*, No. 184, 64 pp.

MS, 1943. Report on 1943 investigations. *Ibid.*, No. 370, 65 pp.

1944. Structure deposition and quality of oyster shell (*Ostrea virginica* Gmelin). *J. Fish. Res. Bd. Canada*, **6**(3): 209–216.

1961. Oyster farming in the Maritimes. *Bull. Fish. Res. Bd. Canada*, No. 131, 158 pp.

MEDCOF, J. C., AND A. W. H. NEEDLER. 1941. The influence of temperature and salinity on the condition of oysters (*Ostrea virginica*). *J. Fish. Res. Bd. Canada*, **5**(3): 253–257.

Comparative Study of the Intraperitoneal Alimentary Tract of Parasitic and Nonparasitic Lampreys from the Great Lakes Region[1,2]

By Helen I. Battle

Department of Zoology
University of Western Ontario, London, Ont.

AND

Kaye Hayashida

Department of Biology
Lakehead College of Arts, Science and Technology
Port Arthur, Ont.

ABSTRACT

The macroscopic and microscopic anatomy of the intraperitoneal alimentary tract of two parasitic species of lamprey, *Petromyzon marinus* and *Ichthyomyzon unicuspis*, and two nonparasitic species, *Entosphenus lamottenii* and *Ichthyomyzon fossor*, are described and compared. In adults of both parasitic species a diverticulum of the anterior mid-gut occurs at the level of the posterior oesophagus; and longitudinal mucosal folds or rugae greatly increase the internal surface of the mid-gut. The course of the mid-gut spiral valve shows species variation, and is more complex in parasitic than nonparasitic adults. Throughout most of the tract tall cilia occur on epithelia over the tips of folds, whereas short cilia form tracts in the fornices. Extra-epithelial tunics are composed of fibro-elastic connective tissue, circular smooth muscle, and a serosa. The four species can be distinguished on the bases of the mucosal folds, spiral valve, and the lining epithelium of the oesophagus.

Atrophy of the tract of both parasitic species commences with the spawning migration, when the epithelium exhibits a characteristic cytolysis with vacuolation of the cytoplasm and peripheral migration of the nuclei. In *Entosphenus lamottenii* atrophy involves initial necrosis of the epithelium and subsequently of the extra-epithelial tunics, both accompanied by massive infiltration of lymphocytes, whereas in *Ichthyomyzon fossor* it is resultant upon autolysis of some of the epithelial cells with progressive reduction in the diameter of the tract without interruption of the lining layer.

INTRODUCTION

Several investigators including Surface (1899), Gage (1928), Applegate (1950), Lanzing (1959), Vladykov and Mukerji (1961), and Sterba (1962) have noted that after the feeding period the alimentary tract of lampreys ceases to function and atrophies. In some nonparasitic European species degenerative processes are initiated even during metamorphosis (Sterba, 1962), and in parasitic species after cessation of feeding and coincident with the hypertrophy of the gonads prior to spawning (Lanzing, 1959). Most studies with

[1]Received for publication September 14, 1964.

[2]These data include a portion of a thesis presented by the second author in partial fulfilment of the requirements for the Master of Science degree at the University of Western Ontario.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

the exception of those of Oppel (1896, 1897) and Krause (1923) have been concerned with gross rather than histological structure and changes in the tract. The present investigation was undertaken to compare the intraperitoneal alimentary tracts of the ammocoetes and adults of the two contrasting biotypes of lampreys, from both the gross and microscopical standpoints. Two nonparasitic species, namely the Michigan brook lamprey, *Ichthyomyzon fossor* Reighard and Cummins, and the American brook lamprey, *Entosphenus lamottenii* (LeSueur) were selected for comparison with two parasitic species, the sea lamprey, *Petromyzon marinus* Linnaeus, and the silver lamprey, *Ichthyomyzon unicuspis* Hubbs and Trautman.

METHODS AND MATERIALS

Ammocoetes and adults of *E. lamottenii*, *I. fossor*, and *P. marinus* were collected from 1956 to 1963 from Big Creek, Norfolk County, and the Saugeen River, Southampton, Ontario. Vladykov's (1950, 1960) descriptions of larvae were followed for identification of species. Adult *I. unicuspis* were taken near Port Burwell and from the north shore of Lake Superior in 1957 and 1963.

Lampreys not fixed in the field were maintained in the laboratory in 45-gal well-aerated aquaria containing about 3 inches of river mud covered by coarse sand, gravel, and approximately 6 inches of water. The aquaria were given maximum exposure to sunlight to induce algal growth to provide food for the ammocoetes. Mortality was less than 10% for periods of 15 months and metamorphosis occurred under these conditions. Rainbow trout (*Salmo gairdneri* Richardson) and goldfish (*Carassius auratus* Linnaeus) approximately 30 cm in length served as food sources for the parasitic species.

For histological preparations, lampreys were anaesthetized lightly in 2% ethyl urethane and fixed in Bouin's picro-acetic-formalin. Individuals less than 140 mm in length were fixed *in toto*, the body wall being slit to permit ready access of the fixative to the viscera. The digestive tracts of larger specimens were removed and fixed in small segments. The material was embedded in Tissuemat of melting point 60–62°C, and sectioned at 7 μ. Sections were prepared through representative levels of the alimentary canal, mounted serially, stained with Ehrlich's alum haematoxylin using Triosin as a counterstain, and with Mallory's Triple Stain.

The course of the spiral valve of the mid-gut was reconstructed from gross transverse sections of the tract cut at intervals of five somites.

The relative secretory-absorptive surface of the anterior mid-gut of ammocoetes and adults was estimated from transverse sections, by determining the ratio of the linear measurement of the mucosal epithelium bordering the lumen to the circumference at the serosa. Microscopical preparations of the mid-gut immediately posterior to the liver were projected at a magnification of 200 diameters and measurements were made by means of a map measure with a revolution counter. The ratio of internal surface to circumference has been termed the I/C ratio.

MACROSCOPIC ANATOMY OF THE ALIMENTARY CANAL

AMMOCOETE

From the standpoint of gross structure, the alimentary tracts of the three species of ammocoetes examined, namely, *P. marinus*, *E. lamottenii*, and *I. fossor*, are almost identical (Fig. 1). The mouth overhung by the oral hood leads to a buccal cavity which is bounded posteriorly by a flap-like

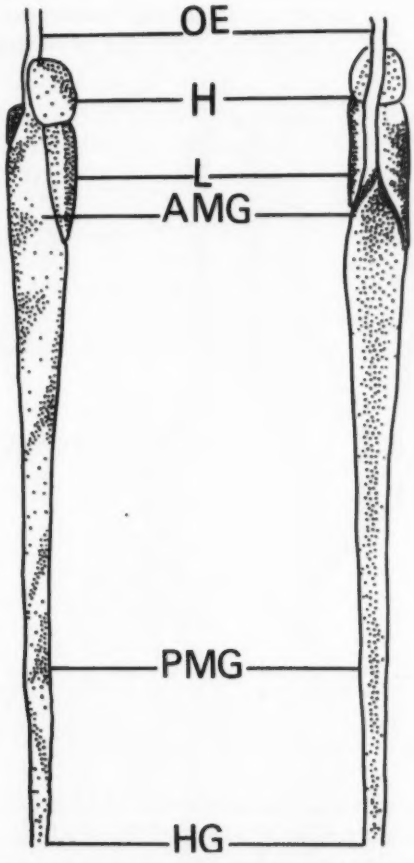


FIG. 1. Dorsal view of the intraperitoneal alimentary canal of *P. marinus*; 120-mm ammocoete on the left and 170-mm adult on the right. AMG, anterior mid-gut; H, heart; HG, hind-gut; L, liver; OE, metabranchial oesophagus; PMG, posterior mid-gut.

velum composed of right and left halves guarding the entrance to the tubular pharynx. Just caudad to the seventh pair of gill pouches at the level of the heart the pharynx merges dorsally into the narrow tubular metabranchial

oesophagus (Sterba, 1962) or fore-gut. The conical ventricle of the heart is completely encircled by the rounded anterior end of the single-lobed liver which then tapers sharply to the right (Fig. 2). A conspicuous greenish-colored gall bladder is partially embedded in the anterior dorsal aspect of the liver. The oesophagus adheres closely to the anterior third of the dorsal surface of the liver, while posteriorly it lies in a dorsal concavity of the latter. Somewhat anterior to the caudal margin of the liver, the tract abruptly dilates to approximately three times the diameter of the oesophagus (Fig. 1, 2) and receives the bile duct on its left margin, thus marking the anterior end of the mid-gut or intestine. The mid-gut progressively decreases in diameter to within a short

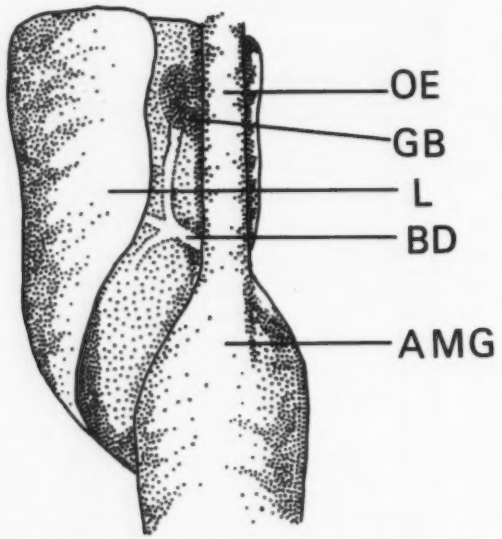


FIG. 2. Ventral aspect of the alimentary canal of ammocoete of *P. marinus* (160 mm) showing oesophagus merging into anterior mid-gut with liver displaced to the right. AMG, anterior mid-gut; BD, bile duct; GB, gall bladder; L, liver; OE, oesophagus.

distance of the anus where it passes without gross demarcation into a short hind-gut. Immediately anterior to the anus the hind-gut receives the pronephric ducts on either side and is now referred to as a cloaca (Fontaine, 1958). Dorsal and ventral mesenteries are lacking except at the level of the hind-gut.

A broad mucosal fold, the spiral valve or typhlosole, extends into the lumen of the mid-gut. It originates from the left wall of the anterior mid-gut (Fig. 4) and progressively decreases in height caudally, disappearing at the junction of mid-gut and hind-gut. In both *E. lamottenii* and *I. fossor* its insertion follows a straight course before undergoing a torsion to the mid-ventral line along the posterior half to third of the mid-gut. In *P. marinus* the insertion

anteriorly lies only slightly to the left of the mid-ventral line. It follows a somewhat irregular course between the mid-ventral and mid-left wall of the gut, exhibiting 2 or 3 torsions before passing along the mid-ventral wall. Daniel (1931) has referred to the expanded anterior portion of the intestine of the ammocoete as the "median valvular intestine," and the tapering region the "post-valvular intestine." In the species described here the former would refer to the complete mid-gut, the latter to the hind-gut.

Recently-Metamorphosed Adult

The alimentary tracts of the adults of the four species of lamprey exhibit fundamentally the same anatomical relationships. The tract of *P. marinus* remains functional for a period up to 2 years after metamorphosis (Applegate, 1950) and decreases in diameter only on attainment of sexual maturity (Surface, 1899; Gage, 1928). Since *E. lamottenii* and *I. fossor* cease to feed at metamorphosis and the digestive tract is nonfunctional or commences to show degenerative changes shortly after metamorphosis (Vladykov, 1949), the following description is applicable to recently-metamorphosed individuals only.

Immediately dorsal to the tongue at the posterior end of the buccal funnel a small mouth leads into an enlarged buccal cavity, and thence into a narrow

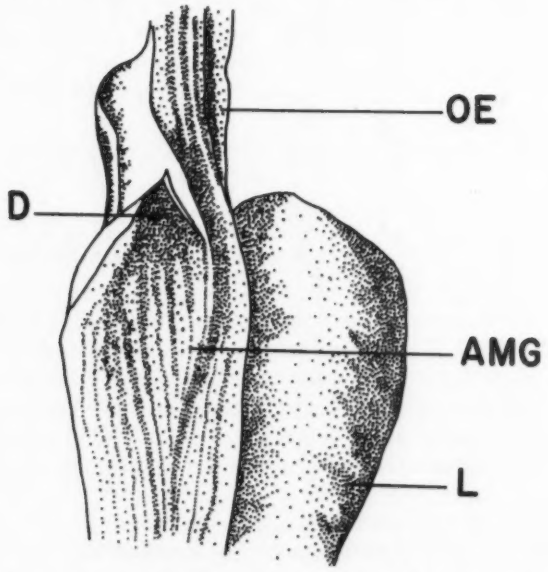


Fig. 3. Dorsal view of alimentary tract of recently-metamorphosed adult (160 mm) of *P. marinus* showing the diverticulum or caecum at the junction of oesophagus and mid-gut. AMG, anterior mid-gut; D, diverticulum; L, liver; OE, oesophagus.

median tube, the epibranchial oesophagus, which arose during metamorphosis by a lengthening of the larval gullet or metabranchial oesophagus dorsal to the pharynx (Sterba, 1962). It continues as the metabranchial oesophagus which occupies the mid-dorsal concavity of the anterior half of the liver. The serosa along the right surface extends into a ligament passing to the dorsal surface of the liver. In both parasitic species, *P. marinus* and *I. unicuspis*, the left wall of the posterior end of the metabranchial oesophagus bears a crescent-shaped thickening (Fig. 3) which is an anteriorly directed diverticulum or intestinal caecum (Fontaine, 1958) of the mid-gut. No corresponding structure is present in the nonparasitic species. At the level of the posterior half of the liver the diameter of the gut increases to approximately three times that of the oesophagus, marking the anterior end of the mid-gut. The mid-gut gradually decreases in diameter as it passes posteriorly in the mid-ventral coelom and merges imperceptibly into the short hind-gut. The cloaca does not persist in transformed adults, the anus and urogenital papilla now opening

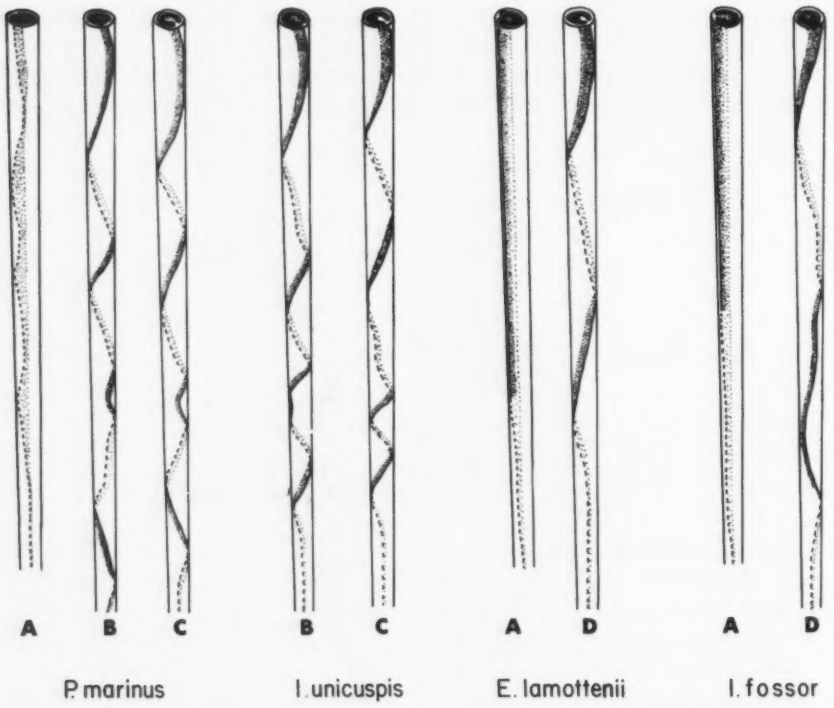


FIG. 4 Diagrammatic representation of the course of the spiral valve of the mid-gut of ammocoetes and adults of four species of lamprey. Continuous line represents insertion of valve along dorsal half of alimentary canal; interrupted line represents insertion along ventral half of alimentary canal. A, ammocoete; B, feeding adult; C, mature migrant; D, recently-metamorphosed adult.

independently (Fontaine, 1958). As in the ammocoete, dorsal and ventral mesenteries are lacking except at the level of the hind-gut.

The spiral valve of the mid-gut in adults (Fig. 4) follows a more complex pathway than that of the ammocoete, presumably as a result of torsion and differential growth of the tract. In all four species the point of origin of the valve is the right dorsal quadrant of the anterior mid-gut wall. It progressively decreases in height as it follows a spiral pathway which is characteristic for each species; and terminates its course in the mid-ventral wall a short distance anterior to the hind-gut. In *P. marinus* the valve when viewed from the anterior end follows a clockwise pathway for two complete revolutions; then after some minor irregularity reverses its course for one and one-half revolutions. In *I. unicuspis* its course covers almost four clockwise revolutions. Although the two nonparasitic species do not feed as adults nevertheless the course of the spiral valve is more complex than in the ammocoete. In *E. lamottenii* it executes one and one-half clockwise revolutions while in *I. fossor* it follows a similar pattern except that the path becomes reversed midway in the last half revolution.

The liver consisting of a single lobe appears reddish-orange in recently-metamorphosed individuals. Neither a gall bladder nor a bile duct is present, both having disappeared during metamorphosis as in *Lampetra fluviatilis* (Krause, 1923; Sterba, 1962). The pancreas in lampreys is not present as a distinct organ, but is represented by patches of what are probably endocrinal acini within the wall of the anterior mid-gut adjacent to the liver, and in parasitic species over the anterior margin of the diverticulum as well (Krause, 1923; Boenig, 1929; Barrington, 1945; Fontaine, 1958).

MICROSCOPIC ANATOMY OF THE ALIMENTARY CANAL

Parasitic Species

Petromyzon marinus

Ammocoete. The microscopic structure of the alimentary tract of the ammocoete shows only minor variations over length ranges from 60 to 150 mm.

In addition to the spiral valve which extends along the length of the mid-gut there are characteristic longitudinal mucosal folds or rugae. Three or four heavy folds are present in the metabranchial oesophagus (Fig. 5) and five or six in the hind-gut (Fig. 6). The spiral valve of the mid-gut in sectional area appears as a horseshoe-shaped typhlosole (Fig. 7) enclosing the large intestinal blood vessels.

The wall of the alimentary tract is composed of a mucosa consisting of epithelium resting upon a basement membrane and a fibro-elastic connective tissue lamina propria, a connective tissue submucosa sometimes indistinguishable from the latter, a tunica muscularis of circularly-arranged smooth muscle fibres which form a complete layer only in the region of the hind-gut, and a serosa. The epithelial lining along the course of the tract varies with respect

to cell types and arrangements. The stratified cuboidal epithelium of the central oral cavity merges into a thin stratified squamous layer which lines most of the pharynx, with the exception of the mid-dorsal and mid-ventral folds where ciliated simple columnar and pseudostratified types occur. Ciliated pseudostratified columnar epithelium with numerous mucous cells forms the lining of the oesophagus (Fig. 8). Ciliated simple columnar epithelium covers the typhlosole (Fig. 7) of the mid-gut as well as the opposing wall; pseudostratified columnar epithelium occurs in the lateral grooves or fornices. The epithelium of the anterior hind-gut is ciliated simple columnar (Fig. 6), and that of the posterior hind-gut and cloaca stratified columnar which merges into stratified cuboidal epithelium continuous with the adjacent epidermis at the anus. Three types of cells (Fig. 9) are present, tall columnar ones bearing cilia, densely-staining serous or zymogenic cells, and lightly-staining mucous cells. The flask-shaped serous cells which are most abundant in the anterior mid-gut are laden with coarse acidophilic granules. They correspond to those described by Brachet (1897) and by Krause (1923) for *Lampetra*. Barrington (1936) demonstrated their importance as a source of proteolytic enzymes. Vacuoles containing dense spherical basophilic inclusions, resembling unicellular algae occur in the cells of both mid- and hind-gut (Fig. 10). Several species of unicellular algae, including *Chlorogonium* sp. and *Scenedesmus* sp., were identified in frozen sections of the alimentary canal, and in some instances appeared to be in process of being engulfed by the epithelial cells. Throughout the entire gut, the epithelium exhibits active mitosis particularly in the fornices. Spherical cells, 3–5 μ in diameter, which occur among the epithelial cells appear to be migrant lymphocytes from the haemopoietic core of the typhlosole (Fig. 9).

Ciliation of the tall columnar epithelia is present from the oesophagus to the hind-gut. Cilia (4–6 μ) occur primarily in tracts over apical and lateral surfaces of the typhlosole as described by Alcock (1899). In the fornices the apical surface of the cells resembles a thick brush border (1–2 μ). Two regions can be distinguished, an outer lightly staining striated zone and an inner more densely staining one. Electron micrographs (Fig. 11) indicate that the outer region is made up of short cilia; and that the inner layer represents the rootlets of the same. The microvilli of the intestinal mucosa of *Myxine*, as described by Adam (1963), bear some superficial resemblance to these short cilia, but the latter in sectional area exhibit the characteristic arrangement of internal longitudinal filaments. Mitochondria occur below secretory vacuoles between the rootlets.

The extra-epithelial tunics are usually very thin and poorly developed. They are composed chiefly of collagenous fibres with relatively few elastic fibers and some smooth muscle. A lamina propria, when present at all, is represented by a very few collagenous fibers immediately beneath the basement membrane. The tunica submucosa consists of an inner layer of highly vascularized, loose fibro-elastic tissue, and a thicker moderately dense peripheral layer. The latter layer is thickest in the oesophagus and the hind-gut.

Areolar connective tissue containing the large intestinal blood vessels and an haematopoietic centre comprises the core of the typhlosole. The circularly arranged smooth muscle fibers are embedded within the outer margin of the submucosa. Oppel (1897) describes the muscularis as being composed of an outer longitudinal and an inner circular layer, with the latter being relatively thick in the hind-gut and very thin in both the oesophagus and the mid-gut. It has not been possible to establish the presence of longitudinally arranged smooth muscle fibres in the ammocoete. The entire gut within the coelomic cavity is covered by a very thin layer of flattened mesothelial cells which adheres to the smooth muscle by connective tissue fibres. This serosa appears considerably thicker in the region of the hind-gut due to a transition from a squamous to cuboidal mesothelium, as well as an increase in the connective tissue.

RECENTLY-METAMORPHOSED ADULT. The alimentary tract undergoes considerable modification during metamorphosis especially with regard to increasing complexity of the longitudinal mucosal folds. Low irregular folds extend into the lumen of the epibranchial oesophagus and become moderately tall as they are continued into the metabranchial oesophagus (Fig. 12). At the level of the anterior mid-gut, they increase in height and number, merging with those of the diverticulum. The posterior end of the oesophagus is marked on the right by the fusion of two folds which form the spiral valve of the anterior mid-gut. Alternating high and low longitudinal folds (40–85+) line the whole mid-gut including the surface of the spiral valve (Fig. 13). These folds progressively decrease in height posteriorly becoming few in number and broad as they continue into the hind-gut (Fig. 14).

The mucosa, submucosa, muscularis, and serosa comprising the wall of the gut show relatively few changes from those of the ammocoete. The extreme anterior end of the oesophagus is lined with stratified cuboidal epithelium, but pseudostratified columnar cells characterize the remainder of it. The epithelium of the mid-gut and the diverticulum is largely simple columnar except in the crypts where it becomes pseudostratified. In the anterior mid-gut, long cilia occur in tracts over the folds, and short cilia in the crypts. In the diverticulum, posterior mid-gut, and hind-gut, the arrangement is more irregular, where wide bands of short cilia occur intermittently with narrower bands of long cilia, the latter always covering the tips of the folds. Mucous cells occur in the oesophageal epithelium, the diverticulum, the mid-gut, and hind-gut while serous cells with coarse acidophilic secretory granules are most abundant in the anterior mid-gut and diverticulum, but also extend as far as the hind-gut. Lymphocytes have impregnated the epithelium, even appearing within the cytoplasm, but cellular inclusions such as those occurring in the ammocoetes are not observed in any part of the tract.

FEEDING ADULT. The diameter of the entire tract has increased considerably over that of recently-metamorphosed individuals. Vladykov and Mukerji (1961) record a width of as much as 27 mm with an average of 9 mm immediately posterior to the liver, in actively feeding half-grown specimens.

TABLE I. Ratio of internal surface to circumference (I/C)[a] for transverse sections of anterior mid-gut of lampreys at various stages.

Species	Stage	Length	Sex	I/C ratio
		mm		
P. marinus	Ammocoete	60	?	1.2
	Ammocoete	125	♀	1.3
	Post-metamorphosis	160	♀	7.3
	Feeding adult	167	♀	11.4
	Migrant adult	360	♀	6.9
	Spawning adult	430	♂	5.6
I. unicuspis	Feeding adult	295	♂	10.6
	Spawning adult	240	♂	4.5
E. lamottenii	Ammocoete	60	?	1.1
	Ammocoete	117	♂	1.2
	Post-metamorphosis	160	♂	3.3[b]
		163	♂	4.2[b]
	Mature adult	184	♂	2.2[c]
		163	♀	1.0[d]
I. fossor	Ammocoete	135	♀	1.1
	Adult	146	♀	0.7

[a]Data obtained from linear measurements of internal surface and circumference made by means of a map measure with a revolution counter on outline drawings (200 ×) of histological transverse sections.
[b]Metamorphosed in April and May 1957 after 7 months in laboratory tanks.
[c]Adult maintained in laboratory tank September and October 1957.
[d]Adult maintained in laboratory tank October to January 1958.

The longitudinal mucosal folds of the oesophagus are taller and have become more numerous. Those of the anterior mid-gut (Fig. 15) are filamentous and sometimes branched, while those of the posterior mid-gut (Fig. 16) are relatively unchanged. Due to a reduction in the connective tissue core, the typhlosole also appears filamentous and less bulbous.

The epithelium of the folds of the mid-gut and anterior hind-gut is simple columnar and that of the crypts is pseudostratified columnar. Many epithelial cells of the anterior mid-gut show evidence of being serous secretory (Fig. 17), but mucous cells are also present. Masses of partially digested connective tissue and muscle together with numerous nucleated erythrocytes in various stages of cytolysis are present in the lumen of the anterior mid-gut (Fig. 15). The large numbers of serous cells would seem to indicate that the anterior

mid-gut and diverticulum of the adult are of primary importance in digestion as in the ammocoete (Barrington, 1936). The apices of many cells of the posterior mid-gut (Fig. 18) are translucent and their reaction with Mallory's Triple Stain identifies them as mucous secreting. Long cilia form a dense covering on the apices of the folds (Fig. 17), although in the posterior mid-gut and anterior hind-gut tracts of short cilia predominate elsewhere.

MATURE MIGRANT ADULT. Applegate (1950) described a decrease in the diameter of the alimentary tract consequent upon cessation of active feeding. Initially the tract becomes flattened dorso-ventrally at the level of the liver. Its histological structure is almost identical to that of a feeding individual with the exception of the longitudinal folds of the anterior mid-gut (Fig. 19) which now appear more tortuous. Some erosion is occurring at the tips of the folds. The contour of the typhlosole is not uniform throughout the mid-gut since its attachment to the wall is intermittently broad and filamentous. Cytolytic changes have been initiated in the epithelium of the whole mid-gut. Extensive vacuolation is occurring immediately peripheral to the nuclei (Fig. 20). Many cells show cytoplasmic inclusions which appear to be identical to those present in the ammocoetes and could represent algae inadvertently ingested during migration. The composition and arrangement of the extra-epithelial tunics are similar to those of the recently-metamorphosed and feeding individuals except that they are thicker and denser consequent upon a tonic contraction of the musculature. The haematopoietic tissue now forms a broad band in the submucosa of the whole mid-gut, but is less evident in the typhlosole.

SPAWNING ADULT. Vladykov and Mukerji (1961) recorded a gut width of only 1.5–3 mm for spawning individuals. The main histological change from that of the mature migrant occurs in the mucosa. The longitudinal folds are showing an advanced degree of erosion (Fig. 21). The epithelium especially in the anterior mid-gut has decreased in height (Fig. 22). The nuclei have migrated toward the free surface of the cells, the chromatin is less basophilic than at any other stage, and the cytoplasm is almost completely vacuolated. These changes are similar to the atrophy described by Vasilieva (1961) for the spring *Lampetra fluviatilis* consequent upon prolonged physiological fasting.

ICHTHYOMYZON UNICUSPIS

FEEDING ADULT. The mucosa of the alimentary tract of this species, as in *P. marinus*, is thrown into numerous longitudinal mucosal folds. Those of the oesophagus (Fig. 23) are somewhat less prominent than in *P. marinus*. In the mid-gut alternate tall and low mucosal folds (60–80) are compactly arranged and occasionally are forked at their free tips (Fig. 24). The epithelial lining of the tract appears to be identical with that of *P. marinus* with a single exception: at the posterior level of the metabranchial oesophagus, the epithelium is a heavy nonciliated, stratified columnar type (Fig. 23). Serous secretory cells with coarse acidophilic granules are abundant throughout the diverticulum and mid-gut (Fig. 25).

The extra-epithelial tunics are comparable to those of *P. marinus* except that the tunica muscularis is more prominent although it also is incomplete except for the heavy circularis of the hind-gut.

SPAWNING ADULT. The spawning adult unlike that of *P. marinus* shows relatively little erosion of the longitudinal folds at any level of the tract (Fig. 26). However, cytolysis of the epithelium (Fig. 27) is advanced as indicated by excessive cytoplasmic vacuolation and migration of the nuclei toward the apical surface. Lymphocytes usually present only toward the bases of the epithelial cells are scattered throughout the cytoplasm.

Nonparasitic Species

ENTOSPHENUS LAMOTTENII

AMMOCOETE. From the histological standpoint the alimentary tracts of the ammocoetes of *E. lamottenii* ranging from 60 to 200 mm in length closely resemble those of the sea lamprey.

RECENTLY-METAMORPHOSED ADULT. The adult in this species is nonfeeding (Vladykov, 1949; Trautman, 1957). The following description is based on a male examined in April. The anterior epibranchial oesophagus is flattened dorso-ventrally and its lumen is not patent. At the mid level, narrow longitudinal mucosal folds are present (Fig. 28). The typhlosole of the anterior mid-gut is large and broadly inserted on the wall; longitudinal folds on both the typhlosole and the gut wall are low, blunt, and less in number (20–40) than in *P. marinus* (Fig. 29). The latter folds almost disappear posterior to the liver where the gut has retained the character of the ammocoete. They reappear in the posterior mid-gut as irregular projections, some 12 or more in number. The hind-gut (Fig. 39) in all respects resembles that of *P. marinus*. The epithelium including ciliation and the extra-epithelial tunics of the tract are similar to those of the adult sea lamprey. Inclusions, which resemble species of algae occurring within the lumen of the gut, are present in the apices of the epithelial cells of the hind-gut.

PROGRESSIVE ATROPHY OF THE ALIMENTARY TRACT OF THE ADULT. Atrophy of the alimentary tract was followed throughout the winter in specimens collected in September and maintained in laboratory aquaria. Those examined in October, November, and December were males (155–185 mm in length), all with markedly enlarged testicular follicles; those in January, February, and March were females (145–165 mm in length) with ovaries containing masses of well-developed oöcytes.

The tract of the October specimen is similar to that of the April one except at the level of the hind-gut (Fig. 30). The entire epithelium is necrotic and the lamina propria and submucosa are heavily infiltrated with lymphocytes, while the tunica muscularis appears to be intact (Fig. 31). The lumen is occupied by a fibrous coagulum composed of necrotic epithelium and lymphocytes. More extensive degeneration of the lining of the tract is apparent in the November specimen. The oesophageal folds have become reduced in height (Fig.

32), and the lumen of the anterior mid-gut (Fig. 33, 34) is completely obliterated by a massive accumulation of lymphocytes and necrotic epithelium. Necrosis is spreading to the connective tissue coats and muscularis throughout the whole mid-gut. The lumen of the posterior hind-gut is now completely obstructed by a dense coagulum (Fig. 35) but necrosis has not yet involved the complete muscularis. In the December specimen atrophy has extended anteriorly to include the oesophageal mucosal folds, and peripherally to the tunica muscularis (Fig. 36).

The lumen of the oesophagus of the January specimen (Fig. 37) is obliterated throughout its entire length by a coagulum of necrotic cells and lymphocytes; only the submucosa at the base of the folds and the muscularis appear to be intact. The epithelium of the typhlosole of the anterior mid-gut as well as the adjacent crypts is now low columnar, and necrosis is evident on the opposing wall (Fig. 38). The extra-epithelial tunics of the whole tract particularly in the mid-gut and hind-gut (Fig. 39) are heavily infiltrated with lymphocytes, so much so that the submucosa actually appears to be increased in thickness. In the February specimen, longitudinal mucosal folds throughout the tract have been eroded, although there is a remnant of the typhlosole in the posterior mid-gut. The lumina of both mid-gut and hind-gut (Fig. 40) are now completely obliterated by coagula of necrotic tissue; and the ventral surface of the mid-gut is fused with the liver (Fig. 41). The extra-epithelial tunics are reduced to a few collagenous and muscle fibers, infiltrated with lymphocytes which have also penetrated the liver parenchyma. The wall of the mid-gut of the March specimen is very thin and now almost indistinguishably fused with the liver, which in turn is considerably smaller than in the February specimen.

Apparently necrosis of the tract in *E. lamottenii* may commence either in the oesophagus or the hind-gut and correspondingly proceed posteriorly or anteriorly. There is no indication of coincident involvement of the liver in male specimens examined in October, November, and December; whereas in females in February and March the degenerating mid-gut wall is fused with the liver.

Ichthyomyzon fossor

Ammocoete. The alimentary tracts of ammocoetes of *I. fossor* varying in length from 100 to 135 mm are almost identical to those of *P. marinus* and *E. lamottenii*.

Recently-metamorphosed adult. Leach (1940) noted that at the onset of transformation, the intestine of *I. fossor* is reduced in diameter, contains no food, and resembles a flattened cord. He also found the oesophagus to be a closed collapsed tube posterior to the 2nd or 3rd gill opening. In the specimens described here the lumen of the anterior end of the epibranchial oesophagus is intermittently occluded, and at such levels appears as a solid mass of epithelial cells (Fig. 42). The posterior oesophagus (epibranchial and metabranchial) has a small lumen and is lined with pseudostratified columnar

epithelium (Fig. 43). Whereas longitudinal mucosal folds characterize the mid-gut of the other three species, only the spiral valve is present in *I. fossor*. It is broadly attached to the wall of the gut and hence in section the typhlosole appears wedged-shaped rather than flask-shaped (Fig. 44). The epithelium is simple low columnar to cuboidal and the extra-epithelial coats are present but reduced in comparison to the parasitic species.

PROGRESSIVE ATROPHY OF THE ALIMENTARY TRACT OF THE ADULT. The alimentary tract of a female specimen in February differed from that of the recently metamorphosed adult in that the diameter of the tract has decreased (Fig. 45). This decrease is not accompanied by a massive invasion of lymphocytes as in *E. lamottenii*. It appears to be largely due to autolysis of some cells, since there is no obvious interference with the continuity of the epithelial surface. The typhlosole has become flatter and less prominent, and the extra-epithelial tunics are reduced in thickness (Fig. 45). The lumen of the oesophagus of a female specimen examined in April is completely obliterated by a solid mass of epithelial cells (Fig. 46). The now narrower lumen of the mid-gut (Fig. 47) is lined by simple cuboidal epithelium. There is no evidence that lymphocytes assume a major phagocytic role in the reduction of either the epithelium or of the extra-epithelial tunics, since there is no marked increase in their numbers.

RELATIVE MUCOSAL EPITHELIAL SURFACES OF THE ANTERIOR MID-GUT OF PARASITIC AND NONPARASITIC SPECIES

A comparison of the relative secretory-absorptive area of the anterior mid-gut of the four species was made by determining the ratio of the lining epithelium to the circumference of the tract (I/C ratio) from typical prepared transverse sections. The results are given in Table I. In the three species examined the I/C ratio for ammocoetes is over the range 1.1–1.3. In both parasitic species, *P. marinus* and *I. unicuspis*, the internal surface is greatly increased in recently-metamorphosed individuals and reaches a peak in the feeding adult (I/C ratio of 11.4 for *P. marinus*). The ratio subsequently declines during migration and spawning when the tract is no longer functional and atrophy is initiated.

In the nonparasitic species *E. lamottenii*, even though the adult is non-feeding, the epithelial surface of the recently-metamorphosed individuals may be trebled or almost quadrupled (I/C ratio of 3.3 and 4.2), but shows a decline in mature adults as necrosis sets in. In the *I. fossor* adult, where initial atrophy is largely due to autolysis of some of the epithelial cells, the I/C ratio is actually less (0.7) than that of the ammocoete (1.1).

DISCUSSION

From both the macroscopic and microscopic standpoints the anatomy of the alimentary canal of ammocoetes and adults of the nonparasitic and parasitic species are in general similar, but do exhibit certain differences. The adults

of the parasitic species possess a diverticulum or caecum of the anterior mid-gut. Krause (1923) and Barrington (1945) observed a similar structure in adults of *Lampetra fluviatilis* and Maskell (1931) noted the presence of two temporary diverticula in the ammocoetes of the genus *Geotria* in New Zealand, Australia, and South America. Barrington (1945) suggested that these caeca may demonstrate the tendency of the secretory epithelium to form an outgrowth fore-shadowing the pancreas of higher vertebrates. This would seem significant in view of the fact that acini, probably endocrinal ones of the pancreas, do surround the anterior end of the diverticulum. It might be postulated that the caecum provides for increased secretory epithelium and absorptive area of the anterior mid-gut.

In the adult the extent of the internal secretory and absorptive surface of the alimentary canal is related to the life habits. The mid-gut of adults of the parasitic species has an extensive internal surface area due to the development at metamorphosis of 40–85 longitudinal mucosal folds over the whole wall including the typhlosole. Although the nonparasitic species do not feed as adults, 20–40 low folds do arise in *E. lamottenii* and persist for a short time after metamorphosis. The mid-gut of *I. fossor* resembles that of the ammocoete with a spiral valve as the only internally directed fold. Thus the absence of mucosal folds in the mid-gut of *I. fossor* and their presence in *E. lamottenii* suggest that the latter is less primitive than the former, substantiating a concept put forward by Hubbs (1924).

At the commencement of the spawning migration, parasitic forms cease to feed, whereas nonparasitic species do not feed after metamorphosis (Vladykov, 1949). In both biotypes cessation of feeding is accompanied by degenerative changes. In *P. marinus* and *I. unicuspis*, the initial changes involve a progressive decrease in thickness of the epithelial lining of the tract, as noted by Applegate (1950) for the former species. Vacuolation of the cells occurs together with a migration of the nuclei toward the free surface comparable to that described by Vasilieva (1961) for *Lampetra fluviatilis*. This is accompanied by lymphocyte invasion of the whole epithelial layer. Coincident changes involve contraction of the wall of the entire tract, and in *P. marinus* a degeneration of the apices of the longitudinal folds and ultimately of the entire folds. Atrophy of the tract differs in the two nonparasitic species *E. lamottenii* and *I. fossor*. That of *E. lamottenii* involves necrosis of the lining epithelium spreading peripherally, and accompanied by a massive invasion of lymphocytes. It may be initiated in either the oesophagus or hind-gut; that in *I. fossor* is brought about initially by autolysis of some epithelial cells thus reducing and ultimately obliterating the lumen of the tract without loss in continuity of the epithelial surface.

Algae as food for ammocoetes have been recorded by Creaser and Hann (1929). Inclusions, presumably of algae occurred predominantly in the posterior mid-gut and to a lesser extent in the hind-gut of the four species. Similar inclusions were found in some adults of all species. Mathers (1926) however found no trace of algae in the gut of adult *Entosphenus tridentatus*, a parasitic

species. Such inclusions in the adult are difficult to interpret, since it seems unlikely that algae would serve as a nutrient source in parasitic forms.

ACKNOWLEDGMENTS

The authors are grateful to Drs W.A. Kennedy and J.J. Tibbles and Mr A.H. Lawrie of the Fisheries Research Board of Canada Biological Station, London, Ontario, for collections of material, and for their interest and assistance at all times; to Dr D.A. McLarty, Department of Botany, University of Western Ontario, for the identification of algae; to Mr C.E. Jarvis, Department of Microscopic Anatomy, University of Western Ontario, for preparation of photomicrographs; to Dr L. Threadgold, Queen's University, Belfast, Northern Ireland, for an electron micrograph; and to Mrs M. Moulton and Mr A. Gage, Department of Zoology, University of Western Ontario, for assistance in photography.

REFERENCES

ADAM, H. 1963. Structure and histochemistry of the alimentary canal, pp. 256–288. *In* A. Brodal and R. Fänge [Ed.] The biology of Myxine, Chap. 5. Universitetsforlaget, Oslo, Norway.

ALCOCK, R. 1899. On proteid digestion in ammocoetes. *J. Anat. Physiol.*, **33**: 612–637.

APPLEGATE, V.C. 1950. Natural history of the sea lamprey (*Petromyzon marinus*) in Michigan. *U.S. Fish Wildlife Serv., Spec. Sci. Rept., Fisheries*, No. 55, pp. 1–236.

BARRINGTON, E.J.W. 1936. Proteolytic digestion and the problem of the pancreas in ammocoete larva of *Lampetra planeri*. *Proc. Roy. Soc. London*, Ser. B, **121**: 221–232.

1945. The supposed pancreatic organs of *Petromyzon fluviatilis* and *Myxine glutinosa*. *Quart. J. Micr. Sci.*, **85**: 391–417.

BOENIG, H. 1929. Morphologie und Entwicklung der Pankreas beim Bachneunauge, III Teil, Die Histologie und Histogenese des Pankreas. *Z. Mikrosk. Anat. Forsch.*, **17**: 125–184.

BRACHET, A. 1897. Développement du pancréas et du foie. *J. Anat. Physiol. (Paris)*, **32**: 620–631.

CREASER, C., AND C.S. HANN. 1929. The food of larval lamprey. *Papers Mich. Acad. Sci.*, **10**: 433–437.

DANIEL, F.J. 1931. Features in the development of ammocoetes. *Univ. Calif. Publ. Zool.*, **37**(4): 41–52.

FONTAINE, M. 1958. Formes actuelles, super-ordres des Petromyzonoidea et des Myxinoidea. Tome XIII Traité de Zoologie (Pierre-P. Grassé), pp. 13–172. Masson, Paris.

GAGE, S.H. 1928. The lampreys of New York State. Life history and economics. A biological survey of the Oswego River system. Supp. to 17th Annual Report, State of New York Conservation Department, pp. 156–191. 1927.

HUBBS, C.L. 1924. The life-cycle and growth of lampreys. *Papers Mich. Acad. Sci.*, **4**: 587–603.

KRAUSE, R. 1923. Mikroskopische Anatomie der Wirbeltiere in Einzeldarstellungen. IV Teleostier, Plagiostomen, Zyklostomen und Leptokardier. Walter de Gruyter & Co. Berlin and Leipzig. Pages 764–858.

LANZING, W.J.R. 1959. Studies on the river lamprey, *Lampetra fluviatilis*, during its anadromous migration. Vitgeversmaatschappij Neerlandia-Utrecht, 82 pp.

LEACH, W.J. 1940. Occurrence and life history of the northern brook lamprey, *Ichthyomyzon fossor* in Indiana. *Copeia*, **1**(1949–41):21–34.

MASKELL, F.G. 1931. On the New Zealand lamprey, *Geotria australis* Gray. Part III. The loss of the mid-gut diverticula of the ammocoetes stage at metamorphosis. *Trans. Proc. New Zealand Inst.*, **62**: 120–129.

MATHERS, V.C. 1926. The velar apparatus of *Entosphenus tridentatus*. *Anat. Rec.*, **34**: 55–60.

OPPEL, A. 1896, 1897. Lehrbuch der Vergleichenden Microskopischen Anatomie. Verlag von Gustav Fischer. Jena. Vols. I, II.

STERBA, G. 1962. Die Neunaugen (Petromyzonidae) Band III Handbuch der Binnenfischerei Mitteleuropas. E. Schweizerbart'sche Verlagsbuchhandlung. Stuttgart. Pages 263–352.

SURFACE, H.A. 1899. Removal of lamprey from the interior waters of New York. *4th Ann. Rept., N.Y. Comm. Fish. Game and Forests*, pp. 191–245.

TRAUTMAN, M.B. 1957. The fishes of Ohio. The Ohio State Univ. Press, Columbus. Pages 131–150.

VASILIEVA, N.E. 1961. Functional variability of intestinal epithelium in Baltic lamprey, *Lampetra fluviatilis* L. *Arkh. Anat. Gistol. i. Embriol*, **41**(11): 96–100.

VLADYKOV, V.D. 1949. Quebec lampreys (Petromyzonidae). I. List of species and their economic importance. *Contrib. Quebec Dept. of Fish.*, No. 26, pp. 1–67.

1950. Larvae of eastern American lampreys (Petromyzonidae). 1. Species with two dorsal fins. *Nat. Canadien*, **77**(3–4): 73–95.

1960. Description of young ammocoetes belonging to two species of lampreys: *Petromyzon marinus* and *Entosphenus lamottenii*. *J. Fish. Res. Bd. Canada*, **17**(2): 267–288.

VLADYKOV, V.D., AND G.N. MUKERJI. 1961. Order of succession of different types of infraoral lamina in landlocked sea lamprey (*Petromyzon marinus*). *J. Fish. Res. Bd. Canada*, **18**(6): 1125–1143.

EXPLANATION OF FIGURES

Plate I

FIG. 5–10. Photomicrographs of histological cross sections of the alimentary canal of the ammocoete of *P. marinus* (125 mm). All sections 7μ in thickness and stained with Ehrlich's alum haematoxylin and Triosin. CE, simple columnar epithelium; I, inclusion; L, lymphocyte; LC, long cilia; LP, lamina propria; M, mitochondria; MC, mucous cell; PE, pseudostratified columnar epithelium; R, rootlet; S, serosa; SC, short cilia; SER, serous cell; SM, submucosa; SV, secretory vacuole; T, typhlosole (spiral valve); TM, tunica muscularis.

FIG. 5. Metabranchial oesophagus at level of the heart showing mucosal folds bearing long cilia.

FIG. 6. Anterior hind-gut lined with simple columnar epithelium.

FIG. 7. Anterior mid-gut showing horseshoe-shaped typhlosole with haematopoietic connective tissue core.

FIG. 8. Ciliated pseudostratified columnar epithelium of oesophagus.

FIG. 9. Ciliated pseudostratified columnar epithelium of anterior mid-gut.

FIG. 10. Epithelium of mid-gut showing basophilic inclusions.

FIG. 11. Electron micrograph of apical area of epithelial cell of mid-gut showing short cilia.

Plate II

FIG. 12–20. Photomicrographs of histological cross sections of the alimentary canal of adult *P. marinus*. All sections 7μ in thickness and stained with Ehrlich's alum haematoxylin and Triosin. D, diverticulum; F, food mass; I, inclusions; LC, long cilia; LP, lamina propria; MC, mucous cell; OE, oesophagus (metabranchial); P, pancreatic tissue; SCE, stratified columnar epithelium; SER, serous cell; SM, submucosa; T, typhlosole (spiral valve); TM, tunica muscularis; V, vacuole. (Fig. 12–14, recently-metamorphosed individual (157 mm); Fig. 15–18, feeding adult (167 mm); Fig. 19–20, mature migrant (360 mm).)

FIG. 12. Section showing metabranchial oesophagus with low irregular mucosal folds on the right, diverticulum on the left.

FIG. 13. Anterior mid-gut showing alternating tall and low mucusal folds.

FIG. 14. Hind-gut showing few heavy mucosal folds.

FIG. 15. Anterior mid-gut showing alternating tall filamentous and low mucosal folds.

FIG. 16. Posterior mid-gut showing fewer and heavier mucosal folds than in anterior hind-gut.

FIG. 17. Pseudostratified columnar ciliated epithelium over lateral surface of fold, anterior mid-gut.

FIG. 18. Pseudostratified columnar ciliated epithelium of fold, posterior mid-gut. Apices of cells show mucous secretion.

FIG. 19. Anterior mid-gut showing tortuous tall mucosal folds.

FIG. 20. Pseudostratified columnar epithelium of anterior mid-gut showing algal-like inclusion and initiation of vacuolation of cells peripheral to nuclei.

Plate III

FIG. 21–27. Photomicrographs of histological cross sections of the alimentary canal of *P. marinus* and *I. unicuspis*. All sections 7μ in thickness and stained with Ehrlich's alum haematoxylin and Triosin. C, cilia; D, diverticulum; EF, eroded mucosal fold; L, lymphocyte; LI, liver; LP, lamina propria; N, nucleus; OE, oesophagus (metabranchial); SER, serous cell; T, typhlosole (spiral fold); V, vacuole. (Fig. 21, 22, spawning adult (350 mm) of *P. marinus*; Fig. 23–25, feeding adult of *I. unicuspis* (290 mm); Fig. 26, 27, spawning adult of *I. unicuspis* (280 mm).)

FIG. 21. Anterior mid-gut showing extensive erosion of both tall and low mucosal folds.

FIG. 22. Low columnar epithelium of anterior mid-gut showing nuclei becoming less basophilic, and vacuolation of cytoplasm.
FIG. 23. Section at posterior end of oesophagus (metabranchial) at level of diverticulum.
FIG. 24. Anterior mid-gut showing alternating tall and low mucosal folds.
FIG. 25. Mucosal fold showing densely basophilic nuclei and serous secretory cells.
FIG.26. Anterior mid-gut showing intact mucosal folds.
FIG. 27. Pseudostratified columnar epithelium of anterior mid-gut showing nuclei migrating to free surface, lymphocyte invasion, and vacuolation of cytoplasm.

Plate IV

FIG. 28–36. Photomicrographs of histological cross sections of the alimentary canal of adult (male) *E. lamottenii*. All sections 7 μ in thickness and stained with Ehrlich's alum haematoxylin and Triosin. L, lymphocyte; LI, liver; LP, lamina propria; NT, necrotic tissue; SM, submucosa; T, typhlosole; TM, tunica muscularis. (Fig. 28, 29, recently-metamorphosed individual (160 mm); Fig. 30,31, October adult (185 mm); Fig. 32,33,34,35, November adult (154 mm); Fig. 36, December adult (184 mm).)
FIG. 28. Oesophagus with narrow elongated mucosal folds.
FIG. 29 Anterior mid-gut with low mucosal folds.
FIG. 30,31. Hind-gut showing necrosis of whole epithelial lining and heavy infiltration of lymphocytes into lamina propria and submucosa.
FIG. 32. Oesophagus with some reduction of mucosal folds.
FIG. 33,34. Anterior mid-gut with lumen completely obliterated by necrotic epithelial tissue and masses of lymphocytes. Necrosis has extended to extra-epithelial tunics.
FIG. 35. Hind-gut with lumen obstructed by necrotic tissue. Necrosis extends into tunica muscularis.
FIG. 36. Oesophagus showing complete erosion of mucosal folds and connective tissue tunics but not muscularis.

Plate V

FIG. 37–41. Photomicrographs of histological cross sections of the alimentary canal of adult (female) *E. lamottenii*. All sections 7 μ in thickness and stained with Ehrlich's alum haematoxylin and Triosin. (Fig. 37–39, January adult (163 mm); Fig. 40–42, February adult (146 mm).) C, coagulum of necrotic tissue; EE, eroded epithelium; L, lymphocyte; LI, liver; SM, submucosa; O, ovum; T, typhlosole (spiral valve); TM, tunica muscularis.
FIG. 37. Oesophagus with eroded mucosal folds, coagulum of necrotic tissue obstructing lumen.
FIG. 38. Anterior mid-gut showing some erosion of epithelium on wall opposite typhlosole.
FIG. 39. Hind-gut showing no erosion of epithelium but some invasion of submucosa by lymphocytes.
FIG. 40. Hind-gut with mucosa completely necrotic. Lymphocytes have invaded to margin of tunica muscularis.
FIG. 41. Anterior mid-gut mucosa completely eroded, ventral surface of muscularis fused with liver, which also shows extensive invasion by lymphocytes.

Plate VI

FIG. 42–47. Photomicrographs of histological cross sections of the alimentary canal of adult *I. fossor*. All sections 7 μ in thickness. Fig. 42–44 stained with Mallory's Triple Stain; Fig. 45–47 with Ehrlich's alum haematoxylin and Triosin. MGL, mid-gut lumen; OE, oesophageal epithelium; O, ovum; PE, pseudostratified columnar epithelium; T, typhlosole (spiral valve). (Fig. 42–44, recently-metamorphosed individual (146 mm); Fig. 45, February adult (155 mm); Fig. 46, 47, April adult (145 mm).)
FIG. 42. Anterior end of epibranchial oesophagus showing lumen occluded by epithelial cells.
FIG. 43. Posterior end of epibranchial oesophagus lined by pseudostratified columnar epithelium.
FIG. 44. Anterior mid-gut showing wedge-shaped typhlosole (spiral valve).
FIG. 45. Anterior mid-gut with reduced lumen, flattened typhlosole.
FIG. 46. Oesophagus (metabranchial) with lumen obliterated.
FIG. 47. Reduced anterior mid-gut with narrow lumen, typhlosole no longer evident; epithelium now cuboidal is still intact.

Note: Figures 5–47 follow.

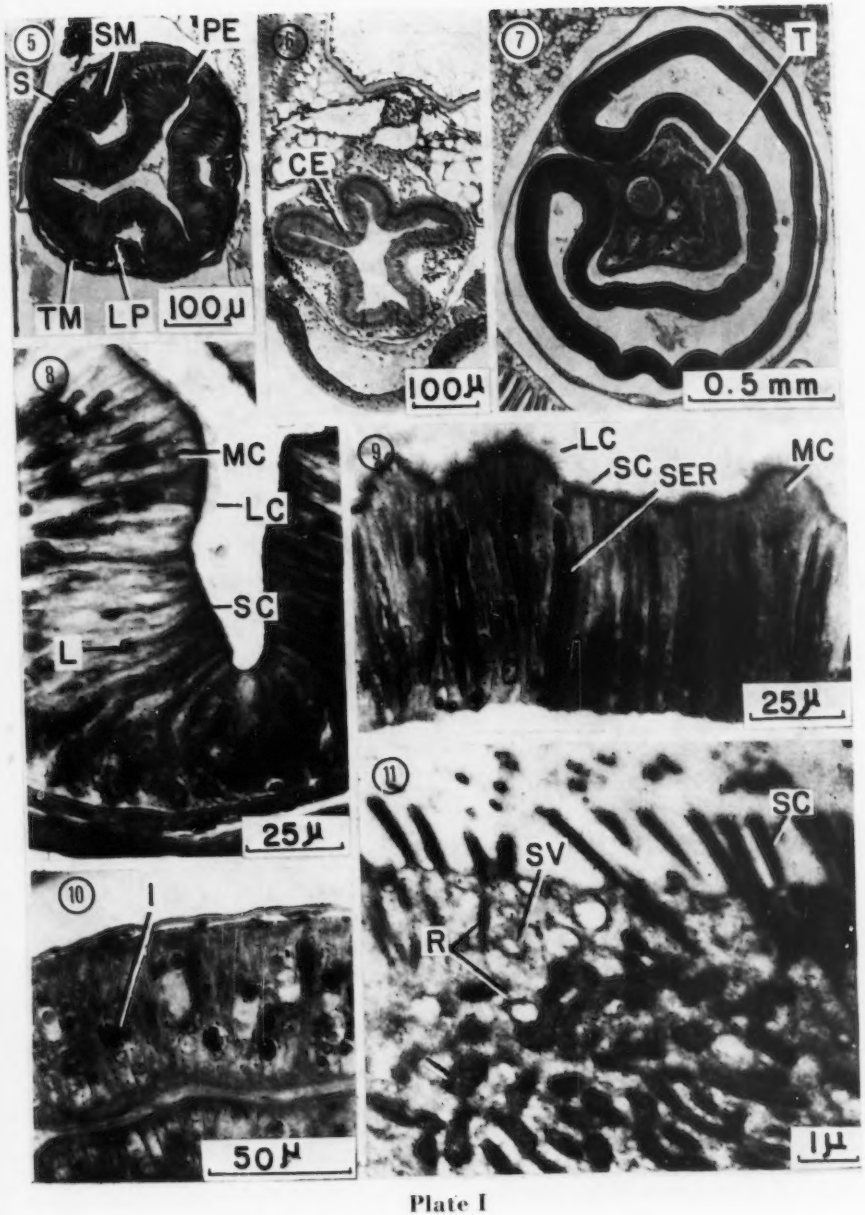


Plate I

Battle and Hayashida — J. Fish. Res. Bd. Canada

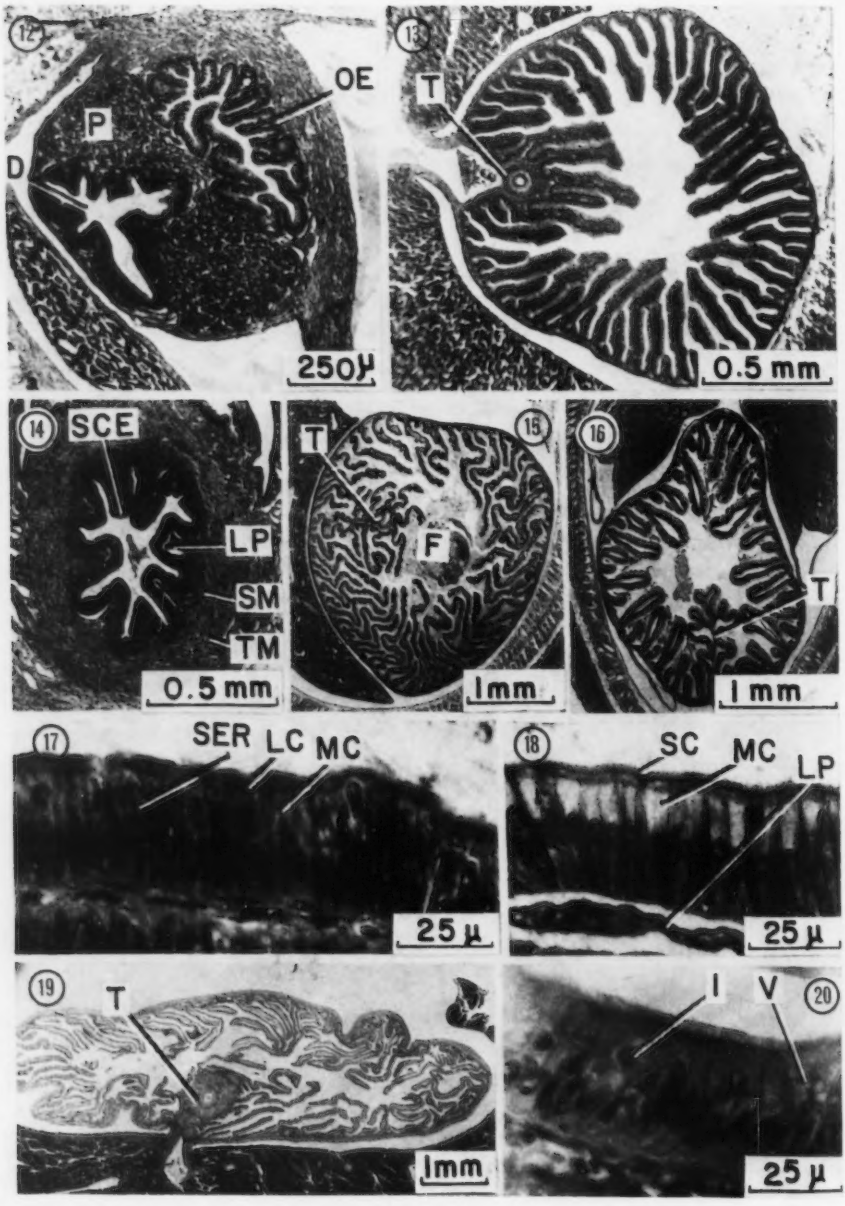


Plate II

Battle and Hayashida — J. Fish. Res. Bd. Canada

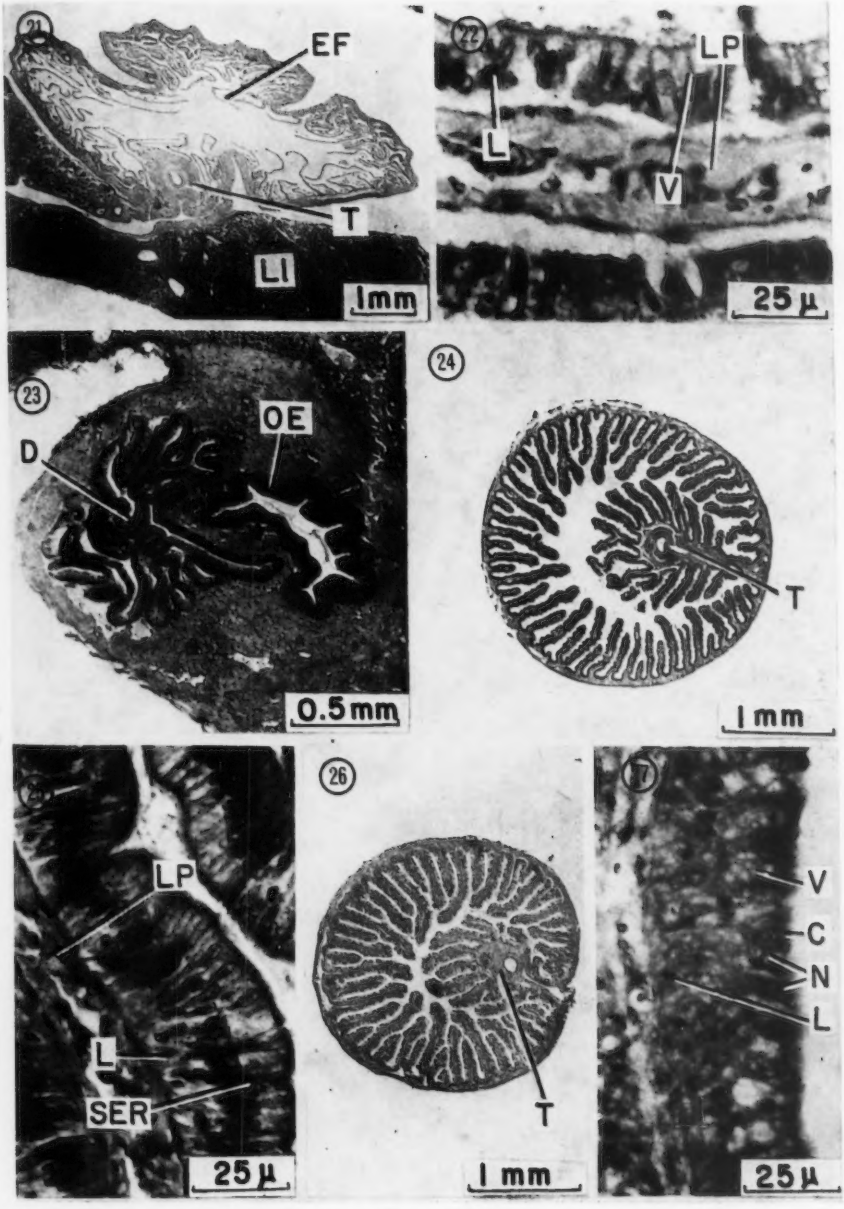


Plate III

Battle and Hayashida — J. Fish. Res. Bd. Canada

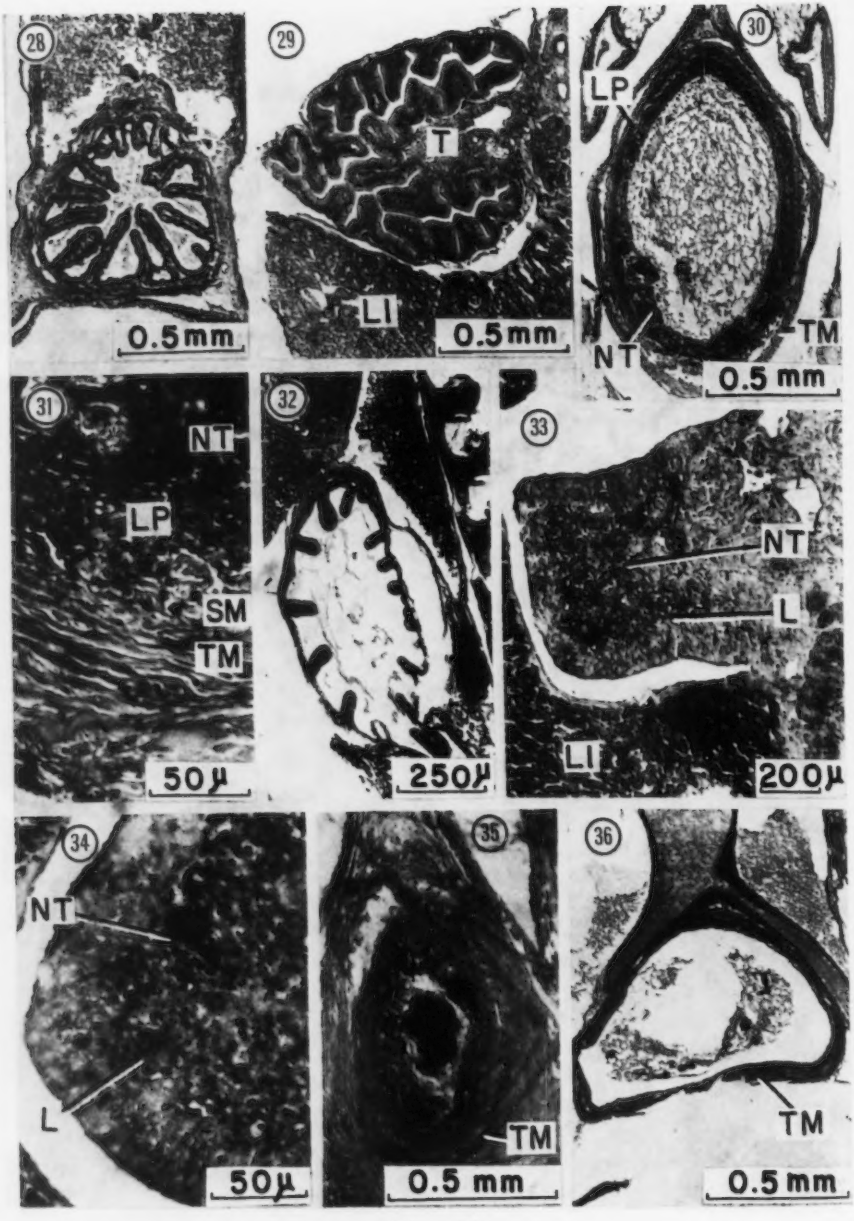


Plate IV

Battle and Hayashida — J. Fish. Res. Bd. Canada

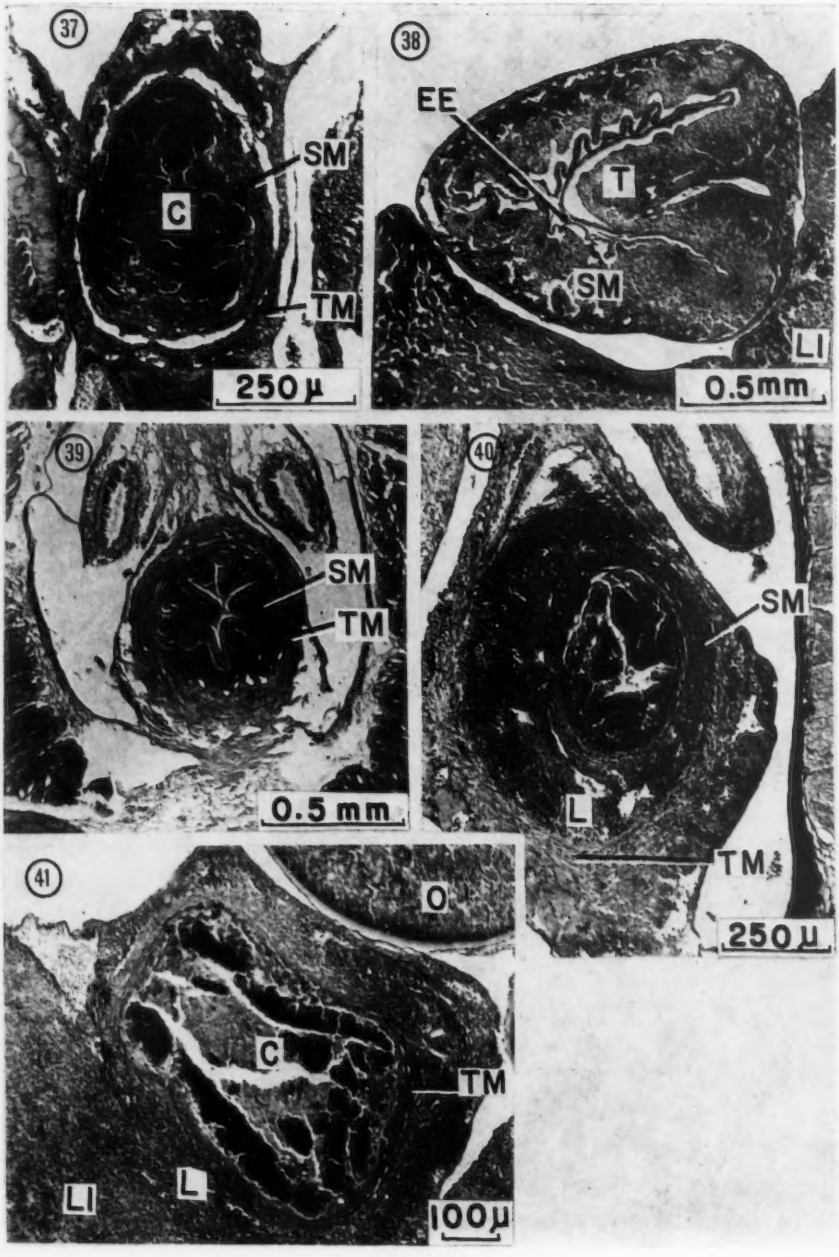


Plate V

Battle and Hayashida — J. Fish. Res. Bd. Canada

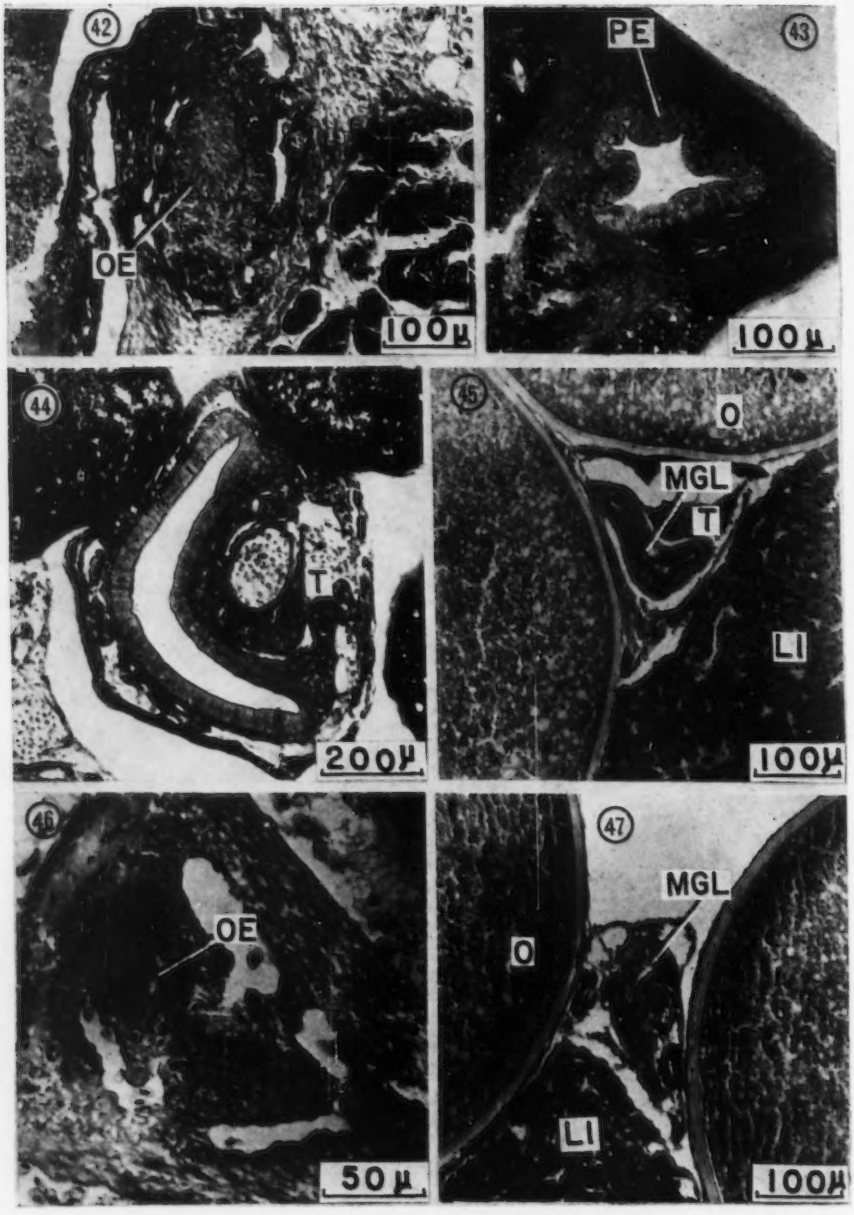


Plate VI

Battle and Hayashida — J. Fish. Res. Bd. Canada

Nucleotides and Related Compounds, Sugars, and Homarine in Shrimp[1]

By H. L. A. Tarr and A. G. Comer

Fisheries Research Board of Canada
Technological Research Laboratory, Vancouver, B. C.

ABSTRACT

Pink shrimp (*Pandalus borealis*) frozen promptly after capture were extracted with perchloric acid and the clear extract, after neutralization with KOH and removal of potassium perchlorate, was subjected to ion exchange chromatography. Glucose, ribose, inosine, inosinic acid, adenylic acid, and a small amount of hypoxanthine were detected. Only traces of hexose phosphates appeared to be present. Homarine was present in moderate concentration and was isolated as crystalline homarine hydrochloride.

INTRODUCTION

The occurrence of certain acid-soluble phosphorus compounds and free sugars in muscles of teleost fishes, and the origin of these compounds, was described in a previous paper (Tarr and Leroux, 1962). The present communication is concerned with the distribution of these compounds and of homarine in shrimp.

MATERIALS AND METHODS

Pink shrimp (*Pandalus borealis*) caught locally by trawl were promptly frozen by placing them in dry ice. Since the commercial fishing operations employed permitted the shrimp to "struggle" before they were frozen, there was obviously ample opportunity for degradation of labile compounds such as ATP.[2]

The nucleotides and related compounds used for reference purposes were the best grades available from Calbiochem, Los Angeles, or from Pabst Laboratories, Milwaukee, Wisconsin.

Homarine hydrochloride was obtained from the Aldrich Chemical Co., Milwaukee, Wisconsin. It was chromatographically homogeneous in solvent systems A and B (see below). The ϵ at 272 mμ was 6400, which is in good agreement with the value of 6325 quoted by Gasteiger *et al.* (1962). The absorption ratios in aqueous solution were: 250/260 mμ, 0.40; and 280/260 mμ, 1.42. The absorption maximum increased only very slightly at alkaline pH values as noted by the above workers.

[1]Received for publication September 30, 1964.

[2]The following abbreviations are used: ATP, adenosine triphosphate; AMP, adenosine 5′-phosphate; and IMP, inosine 5′-phosphate.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

The following solvent systems were employed for paper chromatography at 20°C, using Whatman No. 40 paper unless otherwise stated: A, 85% saturated NH_4HCO_3 (Hems, 1959); B, isobutyric acid–H_2O–28% ammonium hydroxide, 66:33:1 (Zetterström and Ljunggren, 1951); C, isopropanol–conc. HCl–H_2O, 170 ml + 41 ml + H_2O to 250 ml (Wyatt, 1955).

One-hundred-gram portions of frozen shrimp were extracted with cold 0.6*M* perchloric acid, and the extracts treated as in previous work with fish muscle, using the same ion-exchange resin method of separating the various compounds (Tarr and Leroux, 1962). The columns used were 1.4 cm in diameter.

RESULTS

Since separation of nucleotides and sugar phosphates, but not of purine and pyrimidine bases and nucleosides, was determined previously, an initial study was made to ascertain the ability of the ion-exchange system to separate the latter. Twenty micromoles each of adenine, guanine, hypoxanthine, cytosine, thymine, uracil, adenosine, guanosine, inosine, cytidine, thymidine, and inosinic acid were dissolved in 100 ml of 0.6*M* perchloric acid and treated as usual. The elution of the various compounds was monitored by automatic recording of the ultraviolet light absorption of the column eluate and by determining absorption spectra employing a Beckman Model DB recording spectrophotometer. The contents of the tubes containing the various "peaks" were pooled, and the solutions passed slowly through 15 × 1.9 (diam.) cm Dowex 50 × 4 NH_4 resin (100–200-mesh columns). Aliquants of the solutions were evaporated to dryness using rotary evaporators at 40°C. The residues were dissolved in a minimum amount of water and chromatographed either in system A (6 hr ascending development using Whatman No. 3 MM paper) or B (16 hr descending development). The nucleotides were identified by their characteristic absorption spectra in ultraviolet light and by their Rf values.

The results (Fig. 1) show that, with the exception of thymine, cytosine, and uridine, which were eluted simultaneously in the first peak, the various purine and pyrimidine bases and corresponding nucleosides were eluted as separate peaks, and that all preceded IMP. In most instances no attempt was made to determine recovery, since in previous work good recovery of nucleotides had been obtained. However, in two instances where recovery was determined, it was 95 or 100% of the 20 μmoles chromatographed.

Three different experiments were made in which the content of nucleotides and related compounds in shrimp was investigated with similar findings. The results of one experiment are shown in Fig. 1.

The pooled fractions from peak A had absorption ratios which were practically identical with those of homarine (250/260 mμ, 0.41; 280/260 mμ, 1.42). The absorption at 272 mμ indicated that approximately 850 μmoles were present (see below for preparation of homarine from shrimp). Peak B contained hypoxanthine (8 μmoles), C, inosine (92 μmoles), D, IMP (38 μmoles), and E, AMP (43 μmoles). Only very small amounts of ATP plus ADP were found.

If other purines, pyrimidines, nucleosides, or nucleotides were present, the concentrations were too low to permit identification using the present system which in previous work was not found sensitive enough to separate fairly small amounts of nucleotides. Shrimp extract gives a rather high "background" absorption during the first 5 litres of column elution, and this makes identification of minor "peaks" impossible.

Glucose, ribose, and a sugar which appeared from its Rf value in solvent system B to be maltose, were identified in the column "washings". In different experiments 47 and 39 mg of glucose and 8.6 and 9.8 mg of ribose per 100 g of whole shrimp were recovered. The quantities of glucose are rather similar to those which have been found in fish muscle. The shrimp contained quite large amounts of inosine, IMP, and AMP. If these are degraded post mortem to ribose as they are in fish muscle, the reason for the comparatively low ribose content would appear to be their incomplete degradation since little hypoxanthine was found. The influence of post-mortem storage on the content of free sugars has not yet been determined.

Separate experiments were performed and the eluates were tested for hexoses (anthrone reaction) in attempts to determine if hexose phosphates were present. Very small peaks were obtained in the regions where glucose 6- and fructose 6-phosphates are normally eluted. However, the concentrations were far too low to permit adequate identification.

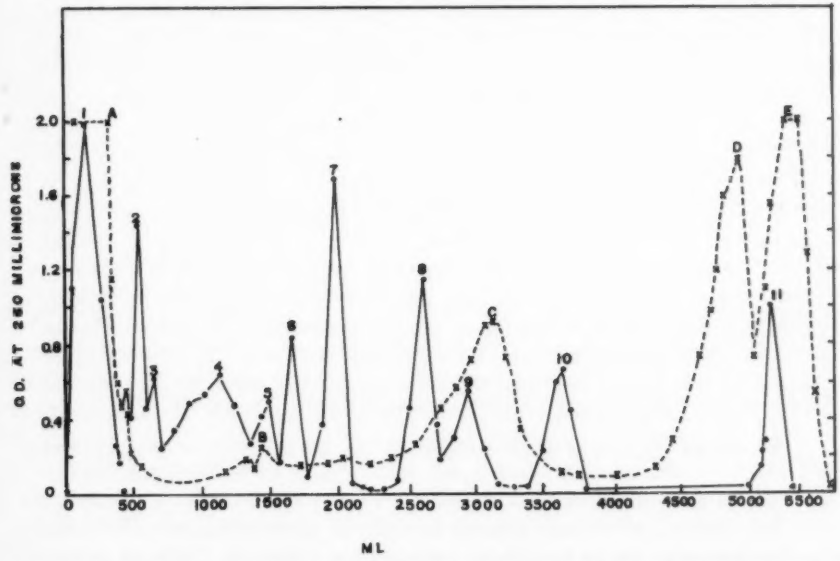


FIG. 1. Ion exchange separation of a mixture of purines, pyrimidines and related compounds (•——•) and of an extract of whole shrimp (x - - - x). 1, Thymine, cytosine, and uridine; 2, thymidine; 3, uracil; 4, adenosine; 5, cytidine; 6, guanine; 7, adenine; 8, hypoxanthine; 9, guanosine; 10, inosine; 11, inosinic acid. A, homarine; B, hypoxanthine; C, inosine; D, inosinic acid; E, adenylic acid.

Preparation of Homarine

Five hundred and forty grams of frozen shrimp were blended with 1080 ml of 0.6*M* perchloric acid, the mixture filtered at 0°C through Whatman No. 31 paper employing suction, and the residue washed on the filter with 400 ml of 0.4*M* perchloric acid. The clear supernate (1720 ml) was adjusted to approximately pH 7.0 with 10*N* KOH (120 ml). After 2 hr at 0°C the potassium perchlorate was removed by filtering through Whatman No. 31 paper by gravity, the filter being washed with 250 ml of H_2O. At this stage absorption determinations at 272 mμ using the method suggested by Gasteiger *et al.* (1960) indicated that about 5000 μmoles of homarine were present.

The solution was evaporated (rotary evaporator, 50°C) to 100 ml, chilled for several hours, and additional potassium perchlorate removed by filtration before running the material through a 20 × 4.5 (diam) cm Dowex 1 × 10 (200–400-mesh) formate column. The column was washed with 3 litres of water to remove the homarine and the eluate concentrated to 250 ml. The clear solution (pH 7.5) was run onto a column of Dowex 50 H^+ (200–400-mesh) resin of similar size to the above and, after washing with 800 ml of H_2O, eluted at 450 ml/hr with a linear gradient of 1 litre of 3*N* HCl into 1 litre of 0.5*N* HCl. Ultraviolet monitoring of the column eluate and paper chromatography (solvent systems A or B) of some of the fractions (after concentration) showed that practically all the homarine was eluted in the first 730 ml.

The clear solution was evaporated to dryness and refluxed for 15 min with 100 ml of *n*-propanol; insoluble material was removed by filtration and the *n*-propanol solution held at 0°C for 16 hr. Further crystalline material was removed by filtering at 0°C. The homarine content of the clear filtrate appeared to be about 4600 μmoles, but the absorption ratios (250/260 mμ, 0.49, and 280/260 mμ, 1.31) were not typical of pure homarine. Three volumes of diethyl ether were added at 0°C and the precipitate allowed to collect overnight. The ether was decanted and the residual gum dissolved in methanol and the solution concentrated to a brownish gummy residue (4.25 g). An equal volume of methanol was added, the solution run along four 46-cm wide Whatman No. 17 papers and developed (ascending) 24 hr at 20°C using solvent system C. The papers were dried overnight in an air current. Two major ultraviolet light absorbing zones were found (Rf about 0.35 and Rf 0.70). The fast-moving zone contained the homarine, and the slow-moving zone small amounts of adenine and hypoxanthine, which were identified by paper chromatography.

The homarine was extracted exhaustively portionwise with 2.5 litres of H_2O. The clear filtrate contained about 2900 μmoles of homarine as indicated by ultraviolet absorption at 272 mμ. The absorption ratios (250/260 mμ, 0.43; 260/280 mμ, 1.39) were similar to those of pure homarine. The solution was evaporated in vacuo to yield a viscous brown residue. This was dissolved in 5 ml of isopropanol in a small flask and held 16 hr at 0°C. The crystalline residue was collected on a small tared sintered glass filter, washed with a little cold isopropanol and dried in high vacuum over H_2SO_4 and NaOH. The yield

was 475 mg of 68% pure homarine hydrochloride (MW 173.6) as determined by ultraviolet absorption of an aqueous solution at 272 mμ. The absorption ratios were 0.42 and 1.45 which are similar to those of pure homarine. The yield at this stage calculated as pure homarine hydrochloride was 323 mg (1860 μmoles). The syrupy filtrate on standing several days at 0°C yielded a further 265 mg of crude homarine (absorption ratios as above; purity 23.4%). This corresponds to 357 μmoles of homarine, or a total yield of 2217 μmoles.

The purest fraction was recrystallized by dissolving in hot *n*-propanol, holding at 0°C overnight and drying in high vacuum over P_2O_5. The product was 95% pure as calculated from the ultraviolet absorption of aqueous solutions at 272 mμ. The absorption ratios were 0.41 and 1.44, and the Rf values in solvent systems A, B, and C, were 0.86, 0.69, and 0.75, respectively, which are identical with those of pure homarine hydrochloride.

DISCUSSION

Homarine was first isolated and described by Hoppe-Seyler (1933), and Gasteiger *et al.* (1960) have recently reviewed the literature concerning the distribution of this compound in invertebrates. It has been found in several species of the phylum Arthropoda, including certain crabs and lobster. The present paper appears to be the first record of its occurrence in shrimp. The concentration present would appear to be about the same as in other Crustacea.

The results indicate that freshly-caught shrimp contain moderate concentrations of glucose and comparatively small amounts of ribose. The origin of these sugars has not been determined. If, as in fish muscle, ribose is formed by enzymic degradation of ATP, then its concentration would presumably increase if shrimp were held several days at 0°C. The concentrations of hexose phosphates were extremely low in comparison with those which are normally found in fish muscle even after several days at 0°C. The presence of moderate amounts of AMP, IMP, and inosine suggest that these arise, as in fish muscle, through rapid degradation of AMP. No other nucleotides were detected.

REFERENCES

GASTEIGER, E.L., P.C. HAAKE, AND J.A. GERGEN. 1960. An investigation of the distribution and function of homarine (N-methyl picolinic acid). *In* Biochemistry and pharmacology of compounds derived from marine organisms. *New York Acad. Sci.*, **90**: Art. 3, 622–636.

HEMS, G. 1959. A mildly alkaline solvent for the isolation, by paper chromatography, of purines, pyrimidines, and their nucleosides and nucleotides. *Arch. Biochem. Biophys.*, **82**: 485–487.

HOPPE-SEYLER, F.A. 1933. Über das Homarin, ein bisher unbekannte tierische Base. *Z. Physiol. Chem.*, **222**: 105–115.

TARR, H.L.A., AND M. LEROUX. 1962. Acid-soluble phosphorus compounds and free sugars in fish muscle and their origin. *Canadian J. Biochem. Physiol.*, **40**: 571–589.

WYATT, G.R. 1951. The purine and pyrimidine composition of deoxypentose nucleic acids. *Biochem. J.*, **48**: 584–590.

ZETTERSTRÖM, R., AND M. LJUNGGREN. 1951. The renewal of phosphate in acid-soluble nucleotides in the liver and brain. *Acta chem. Scan.*, **5**: 291–300.

A Comparison of Catches by 3- and 4-Inch Rings on Offshore Scallop Drags[1]

By Neil Bourne

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

Comparative fishing with offshore scallop drags, knit with 4-inch (102-mm) and the standard 3-inch (76-mm) inside diameter rings, was carried out on Georges Bank in 1959 and 1961. Catches of the two drags were measured to determine the possibility of increasing the annual yield of scallop meats by delaying capture of 5-year-old scallops until they are 6 years old (96–108 mm, shell height). The difference in catches of scallops of this size-range by the two drags was small: the larger ring caught 90% as many as the smaller ring caught. The effect of increased linkage on catches was also measured. A mesh regulation enforcing the use of a 4-inch ring would not give the desired selection.

INTRODUCTION

Since 1955, Canadian landings of sea scallops (*Placopecten magellanicus*, Gmelin) have increased more than eight times. This remarkable increase is attributable to the build-up of an offshore fleet, which has accounted for 80% of the landings since 1950 (Fig. 1). Most of this fleet's effort has been expended on Georges Bank where an active United States fishery has existed since the late 1920's (Premetz and Snow, 1953). Total landings from this area increased slightly from 1950 to 1958, but thereafter rose sharply. Part of this sharp increase in landings was due to a large year-class which entered the fishery in 1959, but Canadian landings increased mainly because of the rapid expansion of the fleet size and a tripling of effort (Table I). Even before this period of rapid expansion, fishermen reported that the size of scallops caught was decreasing. During the period of rapid Canadian expansion, both Canadian and United States industry thought that Georges Bank scallop stocks were being overexploited and that some form of management should be introduced to control the lower limit of scallops being taken.

In the offshore scallop fishery a wide size-range of scallops and a great deal of trash (old shell, gravel, rocks; anything that isn't scallops) are landed on deck. The catch is sorted and the scallops culled. The smallest sizes of scallops that are selected from the catch and shucked (markets) vary from boat to boat but these are seldom less than 95 mm in shell height (distance from the umbone to the ventral margin of the shell). Scallops smaller than 95 mm (discards) are shovelled overboard with the trash.

It was shown that if the age at which scallops are first used by the industry was delayed from 5 years old until they are 6 years old (96–108 mm shell

[1]Received for publication August 5, 1964.

J. Fish. Res. Bd. Canada, 22(2), 1965.
Printed in Canada.

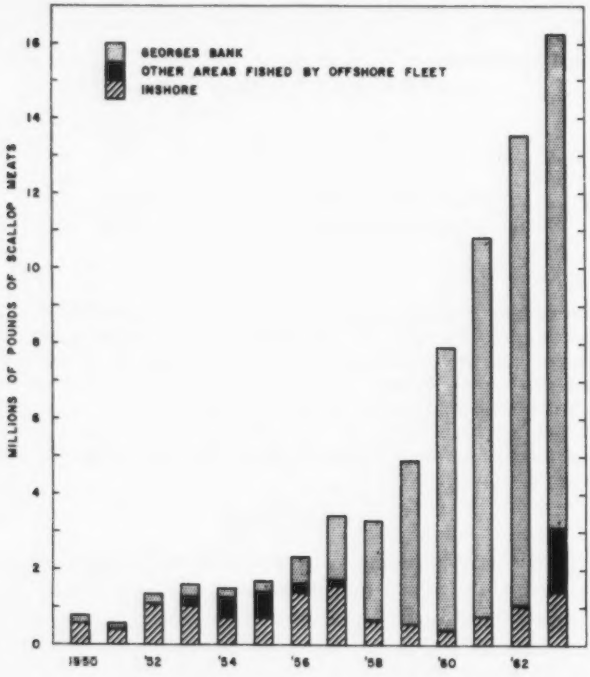


FIG. 1. Landings of sea scallop meats by the Canadian inshore and offshore fleets since 1950.

TABLE I. Landings and effort of United States and Canadian sea scallop fleets fishing Georges Bank, 1951–63.

	Landings of scallop meats in millions of pounds			Effort in days on the grounds		
Year	U.S.	Canada	Total	U.S.	Canada	Total
1951	12.4	0.2	12.6	7,626	–[a]	7,626+
1952	12.1	0.2	12.3	7,742	–[a]	7,742+
1953	16.3	0.3	16.6	10,031	–[a]	10,031+
1954	15.5	0.2	15.7	9,343	–[a]	9,343+
1955	18.3	0.3	18.6	11,619	–[a]	11,619+
1956	17.5	0.7	18.2	12,246	–[a]	12,246+
1957	17.3	1.7	19.0	10,500	1,197	11,697
1958	14.4	2.6	17.0	8,775	1,598	10,373
1959	18.7	4.3	23.0	8,480	2,098	10,578
1960	21.9	7.5	29.4	8,039	2,601	10,640
1961	23.6	10.1	33.7	8,592	3,147	11,739
1962	21.9	13.1	35.0	8,959	4,642	13,601
1963	17.6	13.1	30.7	7,718	5,905	13,623

[a]No data available.

height), there should be an increase in meat yield (Posgay, personal communication). (In the Canadian scallop fishery, only the large adductor muscle, called the "meat" or "eye", is landed.) Estimates of the amount of increase depended on assessments of natural and fishing mortality but increases in yield as high as 25% were predicted.

Unlike the scallop fisheries in Australia and the United Kingdom (Fairbridge, 1953; Mason, 1957) the catch in this offshore fishery is shucked at sea. The most practical way to insure that scallops less than 6 years old (i.e. under 110 mm shell height) are not shucked is to prevent them from being brought on deck. Based on the results of mesh experiments with otter trawls (Clark *et al.*, 1958) it was hoped that the delay in age at first capture could be accomplished by increasing the size of ring used on scallop drags. Previous work by Medcof (1952) and Posgay (personal communication) with scallop gear supported this hypothesis.

The present paper gives the results of two experiments comparing catches of offshore-style drags with 3-inch (76-mm) and 4-inch (102-mm) inside diameter rings. Results of this work have been reported in part at annual meetings of the International Commission for the Northwest Atlantic Fisheries in 1960 and 1962.

METHODS

Gear

The gear and commercial operations of the Canadian and United States offshore scallop fisheries have been fully described by Bourne (1964) and Posgay (1957). Briefly, the standard offshore drag consists of a heavy metal frame 10–13 ft (3–4 m) wide with a bag attached (Fig. 2). Part of the back of the bag is made with rope webbing (rope back) and the remainder of the bag is knit with steel rings. The standard ring at the time of these experiments was made of $\frac{5}{16}$-inch (8-mm) diameter steel wire welded to form a ring with an inside diameter of 3 inches (76 mm) (Fig. 3). Adjacent rings in the bag are joined by split links, made of the same gauge wire but with an inside space of $1\frac{1}{16} \times \frac{1}{2}$ inches (27 × 13 mm). When 3-inch rings are joined in this manner the maximum linear inter-ring space is $3\frac{13}{16}$ inches (97 mm), which is the largest space in the bag (Fig. 3). Rarely are adjacent rings joined by single split links in the Canadian fishery. At the start of a trip, adjacent rings are joined by at least two split links and the maximum linear inter-ring space is $3\frac{1}{2}$ inches (89 mm). As the drag is towed, the links in the bag are ground thin (Fig. 3) but before they break, more links are added. Frequently as many as five links join adjacent rings and the inter-ring space is then reduced to $2\frac{1}{4}$ inches (57 mm) (Fig. 4).

The larger experimental ring was made of the same gauge steel wire but had an inside diameter of 4 inches (102 mm). They were joined with the same type of links. The inter-ring space, however, was larger: $4\frac{7}{8}$ inches (125 mm) when joined by single split links and decreased to $2\frac{13}{16}$ inches (73 mm) when multiple linked with six split links (Fig. 4). Only minor alterations to the drag frame were needed to accommodate the larger ring.

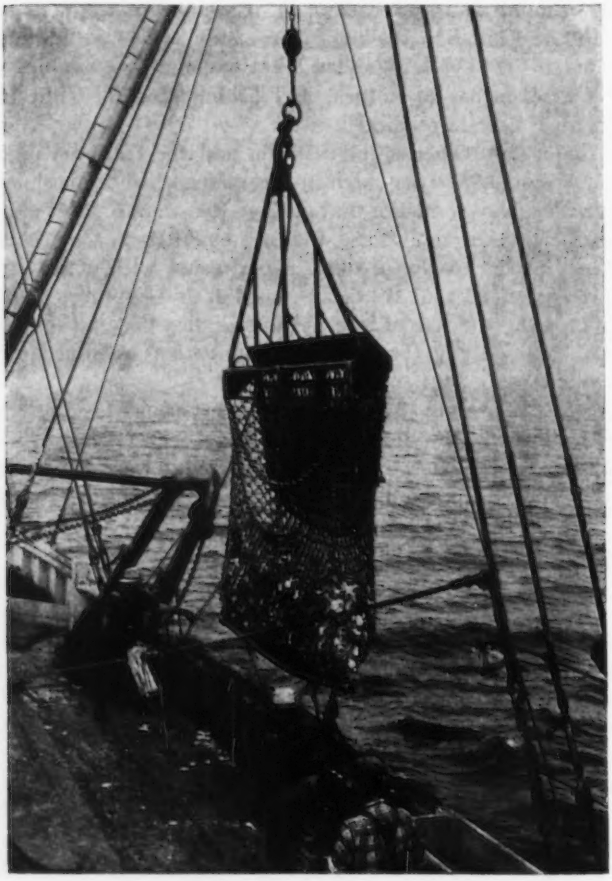


FIG. 2. The 13-ft (3.96-m) offshore scallop drag on M.V. *Cape Eagle*, 1961.

FISHING PROCEDURE

The gear trials were carried out on two commercial scallopers — the M.V. *Aegir* in 1959, which had 12-ft (3.7-m) drags and the M.V. *Cape Eagle* in 1961, which had 13-ft (4-m) drags. Experimental dragging was done in the same area in both years, the northeast peak and northern edge of Georges Bank. All tows were the duration of commercial tows, 20–30 min.

Scallop draggers tow two drags simultaneously, one on the port and the other on the starboard side. In these experiments the 3-inch-ring drag was towed on one side and the 4-inch-ring drag on the other. Both drags cover the same distance and sample the same population. When the catch was dumped, samples from both drags were taken for direct comparison of scallop

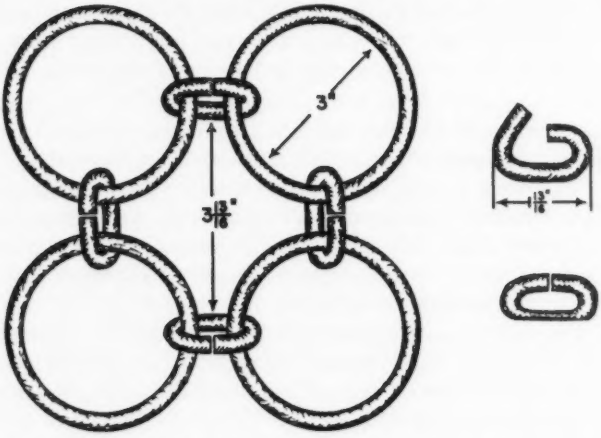


FIG. 3. Diagram illustrating the inter-ring space when 3-inch (76-mm) inside diameter rings are joined by single split links. Top right shows open split link. Bottom right shows closed split link ground thin after use.

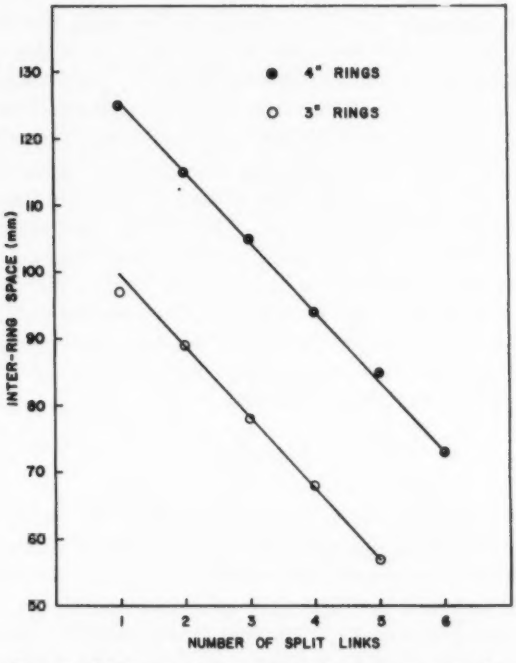


FIG. 4. Maximum linear size of inter-ring space when 3-inch (76-mm) and 4-inch (102-mm) inside diameter offshore scallop rings are joined by increasing number of split links.

sizes in the catches of the two drags. The shell height of each scallop in the sample was measured and the resulting length frequencies were grouped in 5-mm size-groups. The volume of the remainder of the catch was estimated or measured.

In 1959, catches by the two sizes of rings were compared on two trips; 17 comparative tows were made in October and 11 in November. These trials were carried out while the *Aegir* was on commercial fishing trips and since we could not interfere with the operation of the boat, comparisons had to rely on estimates of the size of the catch and on sampling. When the catch was landed on deck, a random bushel sample was selected from each drag and the length frequency of the scallops recorded.

In addition to the above measurements, the number of bushels of market scallops for each drag for an additional 23 tows, 10 in October and 13 in November, was measured. The number of bushels of discards and volume of trash were also estimated for these 23 tows.

No measurements were made of the effect of increased linkage on selection during this work. In fact, the linkage in each bag was quite varied, particularly during the November trip. Also, we were not able to compare the catches of the two drags when the gear was towed on different types of bottom.

In 1961 we chartered the *Cape Eagle* for the trials and the experiments were much more exact. After each tow the volume of the entire catch from each drag was measured and length–frequency measurements recorded for all or for a definite fraction of the scallop catch. Accurate measurements of the volume of trash and the number of discards were obtained for each tow.

The linkage of the 3-inch-ring drag remained the same throughout the experiment in 1961: the top rings were joined by a single link, those on the bottom by two links (denoted as S/D). The 4-inch rings were joined in four different ways during the course of the experiment: top rings joined by a single link and those on the bottom by two links (S/D); two links on top and two on the bottom (D/D); two on top and three on the bottom (D/T) and two on top and four on the bottom (D/Q). All tows were commercial length: 20–30 min duration. An attempt was also made to compare the catches of the two rings on different types of bottom.

RESULTS

1959

We could not estimate the volume of the catches by the two drags accurately in these experiments and hence cannot compare the catches of the two drags on a catch-per-tow basis. The method used to compare the catches was to pool the October and November data and equalize numerically all scallops 105 mm and larger. This gives a correction factor of 1.234. Using this correction factor the number of scallops caught by the 3-inch ring was then recalculated (Appendix Table I). The 105-mm size was selected because the 4-inch ring retains virtually all scallops this size and larger that the 3-inch ring catches.

The catch by the two ring-size drags, using the corrected value for the 3-inch-ring drag, is shown graphically in Fig. 5. It is evident that the larger ring caught fewer discards than the smaller ring. (In the work of both 1959 and 1961 described here, we have used a shell height of 100 mm to arbitrarily divide discards and markets. Scallops smaller than 100 mm are considered as discards, those 100 mm and larger as markets. At the time of these experiments, scallops smaller than 100 mm were rarely picked up by the crews.) If the data are equalized numerically at scallops 100 mm and larger, the resulting curves are much the same as those in Fig. 5, except the difference between the catches is not quite as pronounced. The difference in selection between the two rings is more evident in the October trip than the November trip. This difference was attributed to increased linkage in November.

Further evidence of the difference in catches by the two drags is seen in Table II, which gives the number of bushels of markets and estimates in bushels of discards and trash for the 23 additional tows, 10 in October and 13 in November. The larger ring caught 10% more markets than the standard drag during the October trip and about the same number in the November trip. This decrease in the number of markets caught by the larger ring from the October to the November trip was again attributed to increased linkage.

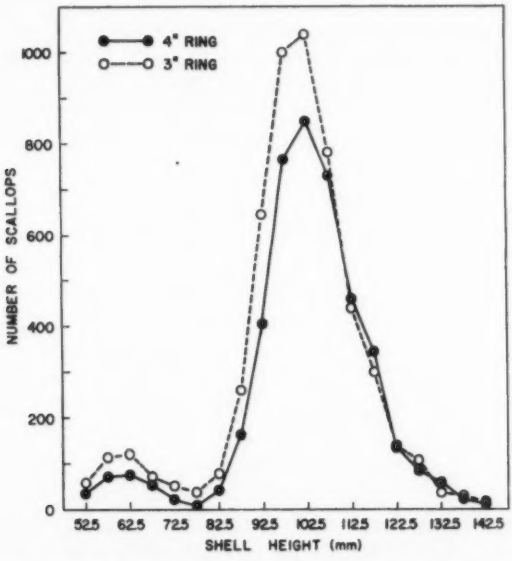


FIG. 5. Size composition (shell height) in 5-mm groupings of scallops caught with a 3-inch (76-mm) ring drag and a 4-inch (102-mm) ring drag on Georges Bank, October and November 1959. Data have been equalized numerically at scallops 105 mm shell height and larger, and the catch by the 3-inch-ring drag adjusted by correction factor. For explanation, see text.

TABLE II. Catch in bushels of market-size scallops, and estimates of numbers of bushels of discard-size scallops and trash by 3-inch (76-mm) and 4-inch (102-mm) ring scallop drags on Georges Bank in October and November 1959.

3-inch ring			4-inch ring		
Markets	Discards	Trash	Markets	Discards	Trash
October 1959					
12	½	½	12	½	½
10	4	5½	11	1	6½
9	1	6½	10	¼	4½
13	4	10	15	3	12
5	2	8	5	1	1
8	2	8	8	1	5
5	½	3	4	–	1
8	2	15	10	2	9
7	2	9	10	1	5
9	2	9	9	1	7
86	20	74½	94	10¼	51½
November 1959					
9	5	7	11	3	6
10	4	10	8	2	5
14	3	10	13	2	6
14	4	3	13	2	12
13	3	13	8	1	7
7	3	9	8	1	6
4½	2	9	4½	1	4
10½	5	12	13	2	5
5	2	8	5	1	5
10	3	11	10	2	8
11	4	12	13	2	8
12	4	12	13	2	10½
5	1	4	4	½	3
125	43	120	123½	21½	85½

The rough estimates of the number of discards and amount of trash caught indicated the 4-inch-ring drag caught 50% fewer discards and 35% less trash. The reduction in discards and trash made the catch easier to handle.

At the time of these trials in 1959 an exceptionally large year-class entered the fishery and dominated it for the next 2 years. Animals of this year-class formed the major part of the catch (Fig. 5) and the larger ring was not tested on scallop populations which had a wide size-range. However, scallops of this dominant year-class were in the size-range which we wished to delay capturing, i.e. 95–109 mm. It is important to note that the larger ring caught 83% as many scallops in this size-range as the smaller ring caught.

1961

COMPARISON OF CATCHES OF SCALLOPS. In the 1961 experiments, the entire catch was measured and the catches of the two drags can be compared directly on a catch-per-tow basis. The number and size of scallops caught by the two drags, for the four linkages of the 4-inch-ring drag, are summarized in Appendix Table II and shown graphically in Fig. 6. Unlike in the 1959 trials no one year-class completely dominated the catch and the catch of scallops by the two ring sizes can be compared for a wide range of shell sizes.

In Fig. 6 the number of scallops caught by the 4-inch ring, in 5-mm size-groups, is expressed as a percentage of scallops in similar size-groups caught by the 3-inch ring. The resulting graphs for each type of linkage of the 4-inch ring show a great deal of scatter. Each curve has an upward trend but none has a steep slope. It is not possible to compare the 50% selection points of the four curves since they rarely touch the 50% line and the points are so scattered that extrapolation of a fitted curve would not give reliable results.

The larger-ring drag caught fewer discards than the standard drag for each of the four linkages investigated (Appendix Table II, Fig. 6). However, the larger-ring drag retained virtually 100% of scallops 105 mm shell height and larger and almost 100% of scallops over 100 mm shell height that the standard ring drag caught. (This validates the "equalization" method used to compare catches of the two ring sizes in 1959.) The experimental drag not only retained 100% of scallops over 105 mm that the standard drag caught, but with each linkage the curves in Fig. 6 extend beyond the 100% line. This indicates that the experimental drag was more efficient than the standard drag at catching markets.

CATCHES OF MARKETS AND DISCARDS. The difference in catch of scallops by the two drags is demonstrated further in Table III. This shows the catch of discards (scallops under 100 mm), markets (scallops 100 mm and larger), scallops under 95 mm, scallops 95–109 mm, and scallops 110 mm and larger by the 4-inch ring expressed as a percentage of the catch of similar size-groups by the standard 3-inch-ring drag. (This is a condensation of Appendix Table III.) When the experimental ring was linked single:double (S/D), double:triple (D/T), and double:quadruple (D/Q), the larger ring caught as many or more markets and considerably fewer discards than the standard ring.

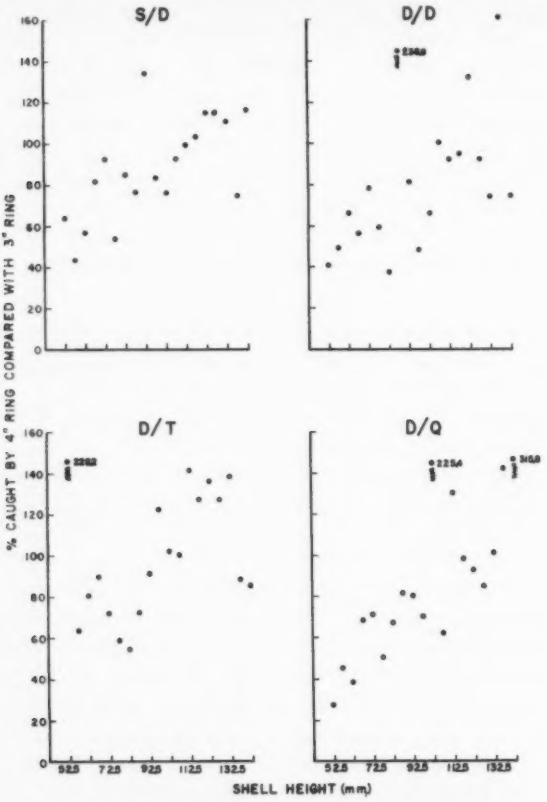


FIG. 6. Catch of scallops in 5-mm size-groups by 4-inch (102-mm) ring drag expressed as a percentage of scallops caught by 3-inch (76-mm) ring drag, when the 4-inch-ring drag was linked in four different ways. Data collected on Georges Bank, August–September 1961.

When it was linked double:double (D/D), the larger ring caught slightly fewer markets and considerably fewer discards than the standard ring. (The data for tows made when the 4-inch ring was linked double:double should be regarded as tentative. Only three tows were made with this linkage and one of the tows was a poor tow.) Pooling the results for all *four* linkages shows the larger ring caught 6% more markets and 24% fewer discards than the standard drag.

The difference in the catch of markets and discards is also evident in Appendix Table III. For each of the four linkages of the 4-inch ring, the catch of this ring contained a higher percentage of markets than the corresponding catch of the standard ring. This is noted even in the case of the double:double linkage. When the data are pooled, the catch of markets comprised 31% of

TABLE III. Catch of five size-groups of scallops by 4-inch (102-mm) ring scallop drag when linked in four different ways, expressed as a percentage of catch of similar size-groups by 3-inch (76-mm) ring scallop drag. Data collected on Georges Bank 1961.

Linkage of 4-inch ring	Discards (under 100 mm)	Markets (100 mm and larger)	Less than 95 mm	95–109 mm	110 mm and larger
S/D	83.07	99.09	83.07	84.78	106.29
D/D	63.36	93.23	66.26	76.27	97.98
D/T	74.25	122.66	71.02	112.51	130.32
D/Q	70.90	113.17	70.91	84.65	105.69
Mean	75.70	105.81	74.75	89.97	111.64

the total catch of scallops of the 4-inch ring and 24% of the catch of the 3-inch ring. This difference may also be expressed on a catch-per-tow basis and it is evident from the Appendix Table III that with the exception of the double:double linkage, the larger ring caught as many or more markets and fewer discards per tow than the standard ring.

CATCH OF SCALLOPS 95–109 MM. It is of interest to compare the difference in catches between the two rings for three size-groups of scallops: scallops smaller than 95 mm, scallops 95–109 mm, and scallops 110 mm and larger (Table III). The difference in catches between the two drags is similar for each linkage except for tows made when the 4-inch ring was linked double: double. When the data for all *four* linkages are averaged, the larger ring caught 74.8% as many scallops in the first category, 90% as many in the second, and 111.6% as many in the third as the standard drag caught. In the size-range where we hoped to delay the age at first capture (95–109 mm), the experimental ring caught 90% as many scallops as the standard ring.

TRASH. There was a marked difference in the amount of trash landed by the two drags (Table IV). This was observed for all four linkages of the 4-inch

TABLE IV. Measurement in bushels of total catch, scallops, and trash by 3-inch (76-mm) and 4-inch (102-mm) ring scallop drags when the 4-inch-ring drag was linked in four different ways. Data collected on Georges Bank, August–September 1961.

Linkage	3-inch S/D	4-inch S/D	3-inch S/D	4-inch D/D	3-inch S/D	4-inch D/T	3-inch S/D	4-inch D/Q	3-inch	4-inch
Number of tows	19	19	3	3	12	12	5	5	39	39
Total catch	836	789¼	129¾	110	568¾	483	280	216¾	1841½	1599½
Catch of scallops (includes clappers)	381¼	379	51	39¾	247¼	226	174½	144	853¾	788¾
Catch of trash	481¾	410½	78¾	70¼	321½	257	105¾	72¾	987¾	810½

ring. The amount of trash landed varied greatly with the type of bottom and the size of the catch. When the data for all four linkages are pooled, the experimental drag caught 18% less trash than the standard ring. The catch of clappers (paired empty shells) is included in the "catch of scallops" in Table IV and was approximately equal for the two rings.

DURABILITY OF LARGER RING. The 4-inch ring in both experiments lasted about as long as the 3-inch ring and was not twisted or distorted any more than the smaller ring.

DISCUSSION AND CONCLUSIONS

VALIDITY OF COMPARISONS

No attempt was made in either the 1959 or 1961 experiment to determine if the fishing efficiency of the two drag frames was the same. In a similar set of experiments, United States investigators did find a difference in efficiency between two drag frames (Posgay, personal communication). However, in the United States experiments there was an obvious physical difference between the two frames. In both our experiments commercial gear, built precisely to the same pattern and in good repair, was used for both large- and small-ring bags. We believe there was no significant difference in the fishing efficiency of the paired drag frames used in either year.

Since the two drags are towed at the same time, they cover virtually the same bottom and sample the same populations. Recent analysis at this Station (to be published separately) has shown that the two tows are indeed duplicate tows and that we can compare the catches of the two drags directly on a catch-per-tow basis. Whether the drags are towed on the port or starboard side of the boat does not affect their fishing efficiency.

COMPARISON OF CATCHES

The difference in catches between the two ring sizes is much less than is observed for most otter trawl selection data with similar differences in mesh size (Clark *et al.*, 1958). One would not expect the overlap in selection range of the 4-inch and 3-inch rings to give such poor results as seen in Fig. 6. An increase from 3 to 4 inches in ring diameter corresponds to an increase of about 2 inches (51 mm) in the size of otter-trawl mesh. Such an increase in the mesh size of otter trawls would give catches with little overlapping and the resulting selection curves would be much steeper than those found here. The 50% selection points are usually readily seen in such data. In the results of our experiments here, the catch curves rarely touch the 50% line (Fig. 6).

The size of the catch undoubtedly affects the amount of selection that takes place. We compared the difference in catches between the two drags for those tows which had less than 30 bushels per tow. (This is a small catch for Canadian boats.) Most of these tows occurred when the experimental drag was linked single:double, since five of these tows were made in an area

of rocky bottom which had little trash. However, the results for these comparisons are similar to those shown in Fig. 6.

Reasons for Poor Selection

The poor difference in selection between the two drags probably results from two main sources. Scallops, unlike fish, do not struggle to escape from drags. Underwater observations of otter trawls have shown that this is important in the escapement of fish from trawls (film of the United States Department of the Interior, Bureau of Commercial Fisheries). When scallops are caught in drags, they close their valves and plug up the rings. Scallops are more easily retained in drags than fish in nets and the only type of sorting that takes place is mechanical sorting.

Probably the major reason for poor escapement of small scallops from scallop drags is the accumulation of trash and scallops in the drag during the tow. Scallop drags, unlike otter trawls, dig into the bottom as they are towed and fill quickly with trash. This trash plugs the drag, drastically reduces mechanical sorting, and virtually eliminates the escapement of young scallops. On some parts of Georges Bank (e.g. southeast part), little trash is brought up in the drags. But on the northern edge and northeast peak, where the bulk of the fishery takes place, as much as 75% of the catch may be trash.

The poor escapement of small scallops because of the accumulation of trash and scallops in the drag agrees with results of otter-trawl mesh selection work. Best selection resulted when catches of fish were small and poorest selection when catches were large.

Comparison with Other Scallop Mesh Selection Experiments

Dickie (1955), using Digby-style gear (MacPhail, 1954) compared scallop catches of drags knit with rings of $2\frac{5}{8}$ inches (67 mm) inside diameter to those knit with $1\frac{1}{2}$ inches (38 mm) inside diameter rings. He obtained much better selection than we did and observed a substantial "savings effect." We cannot explain fully why he obtained so much better selection than we did. A proportionate increase in ring size from the 3-inch ring would require a ring with an inside diameter of $5\frac{1}{4}$ inches (133 mm). The bag on Digby-style drags may remain open better than the bag on offshore drags, which may aid mechanical sorting. Scallop beds off Digby lie on very rocky bottom. If catches were small, the drags may not have plugged up so quickly and better selection resulted.

United States investigators obtained much sharper selection than we did when they compared catches by offshore drags knit with 4-inch (102-mm) and 2-inch (51-mm) inside diameter rings (Posgay, personal communication). All tows in these experiments were of short duration—10 min. Furthermore, their work was carried out on the southeast part of Georges Bank where there is little trash. The small catches and small amounts of trash apparently permitted better selection. In our experiments similar sharp selection may have

taken place in the initial stages of the tow, but the drags soon became plugged and for the remainder of the tow almost no escapement of small scallops took place.

Results for short tows are not applicable to the fishery since commercial tows are longer, 20–30 min, and catches larger. Furthermore, although the southeast part of Georges Bank periodically supports good fishing, the bulk of the fishery takes place on the northern edge and northeast peak where the bottom is very trashy. Since 1957, 70% of the total landings of scallops from Georges Bank have come from this region. If industry adopted the 4-inch ring, catches in the major part of the fishery would be similar to those we have obtained, not to those obtained for short tows.

Increase in Catch of Markets

We cannot explain satisfactorily why the experimental drag caught more markets (scallops 100 mm and over, shell height) than the standard drag. In the 1959 work we felt that the standard drag may have filled before the end of the tow, but not the 4-inch-ring drag. The standard drag would then simply "bulldoze" for the remainder of the tow while the larger ring drag would continue to fish and catch more markets. In the 1961 work we purposely avoided this difficulty by insuring that neither drag was completely filled for any tow. However, in 1961 the experimental drag again caught more markets than the standard drag. Medcof (personal communication) noted the same phenomenon, although not as pronounced as here, when he compared scallop catches by Digby drags knit with $3\frac{1}{4}$-inch (82-mm) and $2\frac{5}{8}$-inch (67-mm) rings; his curve levelled off at about 105%. If a cover were placed over the bag, one could determine if the larger ring drag catches more scallops of all sizes and lets more small scallops escape or if it is simply more efficient at catching large scallops than the standard drag.

Linkage and the Inter-Ring Space

Increased linkage had little effect on differences in sizes of scallops caught by the two rings (Fig. 6). It is difficult to draw curves for the four graphs in Fig. 6. If rough curves are drawn by eye for each of the graphs, none has a steep slope and differences from one to the other are slight. The curve with the steepest slope and presumably best selection occurred when the larger ring was linked double:triple (D/T) but even here the curve is far from the vertical. The inter-ring space in offshore drags apparently is not as important for the escapement of small scallops as Medcof (1952) found for Digby drags. Although the inter-ring space is the longest linear space in the bag on offshore drags, scallops would have to go through it edgewise to escape. This apparently does not happen. Our results indicate that in offshore drags most escapement probably occurs through the ring itself, which would explain why the 4-inch-ring drag retained virtually as many scallops 105 mm and larger and almost as many scallops 100 mm and larger as the standard ring caught.

The percentage of discards (scallops under 100 mm, shell height) in the catch of the 4-inch ring did increase with increased linkage (Appendix Table III). However, for corresponding tows of the 3-inch-ring drag, the percentage of discards in the catch also increased but the linkage of this drag remained the same throughout the experiment. This increase in the percentage of discards caught by both rings can be explained on the basis of where the towing took place. When the 4-inch ring was linked single:double (S/D), nine of the tows were made in areas with few small scallops and little trash. This, of course, would reduce the percentage of small scallops and amount of trash caught by both drags. The scallop populations sampled when the last two linkages were tried, double:triple (D/T) and double:quadruple (D/Q), had a larger proportion of small scallops. Furthermore, these tows were made on trashy bottom. Both these factors would increase the percentage of discards retained by both 3- and 4-inch rings.

We cannot explain one result of the effect of increased linkage. One would expect the percentage of small scallops retained by the larger ring when compared to the catch of similar-size scallops by the 3-inch ring to increase slightly with increased linkage because the inter-ring space and the space of the ring itself will be reduced slightly. However, as can be seen in Table III, this percentage actually decreased with increased linkage of the 4-inch ring (i.e. it decreased from 83% to 71%). The type of bottom, population structure, and length of tow all probably contribute to this phenomenon.

It is apparent that the number of small scallops and amount of trash retained by the larger ring is dependent more on the size-composition of the scallop population and type of bottom than on selection or mechanical sorting.

Assessment

The 4-inch ring did not appreciably alter the catch of 5-year-old scallops (95–109 mm, shell height). It caught 90% as many scallops of this size-range as the standard 3-inch-ring drag caught. These scallops would, of course, be picked up by the crew and shucked. Thus it is not possible by introducing a 4-inch ring to the fishery to delay capturing many 5-year-old scallops until they are 6-year-olds. Since 1961 the size at which scallops are culled has declined and some people feel that the introduction of the 4-inch ring might be of more benefit to the fishery now than it was in 1961. However, scallops smaller than 85 mm are not used by the fishery and the 4-inch ring caught 87% as many scallops in the size-range 85–94 mm as the standard drag caught. Even with this decline in minimum size of scallops culled, the 4-inch ring would not delay capturing a sufficiently large portion of scallops smaller than 110 mm for a significant benefit in the form of increased yield to accrue to the fishery.

Our results show the 4-inch ring would have advantages for the fishery. It caught more markets (scallops 100 mm and larger, shell height) (6% more by number) than the standard drag, fewer discards (scallops under 100 mm,

shell height) (24.3% less by number), and less trash (17.9% less by volume). The latter two advantages would make the catch easier to sort and cull and leave more time to shuck markets.

The reduction in number of discards caught probably has a conservation value to the fishery, although it is probably small. This results from the fact that unlike finny fish (Jean, 1962), most small scallops live when returned to the water. They continue to grow and enter the fishery when they are 5-year-olds. However, under some conditions the number of discards which suffer lethal damage may be as high as 20% (Medcof and Bourne, 1964). A smaller percentage of discards would sustain lethal damage if the larger ring were used.

In 1960 and 1961 a number of Canadian scallop draggers voluntarily used the 4-inch ring, mainly because the catch was easier to sort and cull. In 1962 all reverted to the 3-inch ring because they began fishing on rougher bottom and the 4-inch ring became distorted or broke and left large holes in the bag. (Even the 3-inch ring now used is of heavier gauge steel, $\frac{3}{8}$ inch (9.5 mm).) It might have been to industry's advantage to continue using the 4-inch ring but made with heavier gauge wire.

We can only speculate on what the composition of catches would be if a larger ring, $4\frac{1}{2}$ or 5 inches inside diameter, were used. (United States investigators have made preliminary trials with a 5-inch ring but results are inconclusive (Posgay, personal communication).) Extrapolating from our results described here, we would predict that the catch of 7-year-old scallops (118–125 mm, shell height) and older might increase and the catch of 6-year-olds (108–118 mm, shell height) might decrease slightly. The catch of 5-year-olds (95–108 mm, shell height) would decrease further—perhaps to 75% of that taken by the standard 3-inch-ring drag. (The 4-inch-ring drag decreased it only to 90%.) The amount of trash and number of discards would be further reduced, possibly by another 10–20%.

We have concluded that selection of sea scallops under commercial fishing conditions cannot be controlled by increasing the size of the ring to 4 inches (102 mm) inside diameter on present-style offshore drags. This is particularly true on the trashy bottom of the northern edge and northeast peak of Georges Bank, where the bulk of the landings is caught. Even the use of a $4\frac{1}{2}$- or 5-inch ring would probably not eliminate 50% of the 5-year-old scallops now caught by the standard ring. The accumulation of trash and the fact that scallops don't struggle to escape out of the drag prevent sharp selection taking place. With the present type of gear and commercial practices, a ring-size regulation will not achieve the desired increase in the minimum size of scallops that are shucked by delaying the age at first capture and the subsequent increase in yield will not be obtained.

Future Gear Work Needed

Our results point out the need for future studies on offshore scallop drags. With the exception of a few ring-size selection studies similar to those des-

cribed here, almost no work has been done on the gear since it was first introduced by industry in 1947. We have used underwater television to study the action of Digby-style gear as it was towed on the bottom, but results were of a preliminary nature. We do not know how efficient the offshore drag is at catching scallops, what the action of the drag is as it is towed along the bottom or what is happening to the catch inside the bag during the tow. Scallops can avoid being captured but we must learn more about the effect of approaching drags on their behavior and determine if they can be captured more efficiently. Eventually, it may be necessary to design an entirely new type of scallop drag which would not only be efficient but also selective.

SUMMARY

1. Comparative fishing with offshore scallop drags, knit with the standard 3-inch (76-mm) inside diameter ring and an experimental 4-inch (102-mm) inside diameter ring was carried out on Georges Bank in 1959 and 1961.

2. All tows were of the same duration as commercial tows, 20–30 min.

3. The difference in catches between the two ring sizes in both experiments was less than is obtained in similar mesh experiments with otter trawls with a similar spread in mesh size.

4. The 4-inch-ring drag caught more (6% by number) market-size scallops (scallops 100 mm and larger, shell height) than the standard drag.

5. The 4-inch-ring drag caught fewer (24.3% by number) discard-size scallops (scallops less than 100 mm, shell height) and less (17.9% by volume) trash than the standard drag.

6. Increased linkage between rings had little effect on catches of scallops or on the amount of trash caught.

7. Increasing the size of the ring on the present-style offshore drag to 4 inches inside diameter will not give the desired selection. A mesh regulation enforcing the use of a 4-inch ring would not delay the age at first capture of 5-year-old scallops until they are 6 years old.

8. The need for future studies on scallop drags is pointed out.

ACKNOWLEDGMENTS

I wish to thank Captains George Crouse and Roy Langille and their crews for their willing assistance and co-operation in this work.

I am indebted to Dr J. C. Medcof for helpful suggestions during the course of this work, to Dr F. D. McCracken for assistance in analyzing the data and to both for criticisms of the manuscript. I am grateful to Mr J. A. Posgay of the United States Bureau of Commercial Fisheries Laboratory in Woods Hole, Massachusetts, for reviewing the text and allowing me to view some of his unpublished data. Thanks are also due to Mrs E. I. Lord for assistance

in compiling the data and to Mr R. C. Chandler for his help in the preparation of the figures.

REFERENCES

BOURNE, NEIL. 1964. Scallops and the offshore fishery of the Maritimes. *Bull. Fish. Res. Bd. Canada*, No. 145, 60 pp.

CLARK, JOHN R., FRANK D. MCCRACKEN, AND WILFRED TEMPLEMAN. 1958. III. Summary of gear selection information for the commission area. *Intern. Comm. for the Northwest Atlantic Fisheries, Ann. Proc.*, **8**: 83–98.

DICKIE, L. M. 1955. Fluctuations in abundance of the giant scallop, *Placopecten magellanicus* (Gmelin), in the Digby area of the Bay of Fundy. *J. Fish. Res. Bd. Canada*, **12**(6): 797–857.

FAIRBRIDGE, W. S. 1953. A population study of the Tasmanian "commercial" scallop, *Notovola meridionalis* (Tate). (Lamellibranchiata, Pectinidae). *Australian J. Marine and Freshwater Res.*, **4**: 1–40.

JEAN, YVES. 1962. Discards of cod at sea by otter trawlers. *Fish. Res. Bd. Canada, Biol. Sta., St. Andrews, Circular, General Series*, No. 37, 3 pp.

MACPHAIL, J. S. 1954. The inshore scallop fishery of the Maritime Provinces. *Fish. Res. Bd. Canada, Atlantic Biol. Sta. Circular, General Series*, No. 22, 4 pp.

MASON, JAMES. 1957. Scallop fishing. *Scottish Fisheries Bulletin* No. 6, pp. 10–12.

MEDCOF, J. C. 1952. Modification of drags to protect small scallops. *Fish. Res. Bd. Canada, Atlantic Prog. Rept.*, No. 52, pp. 9–14.

MEDCOF, J. C., AND NEIL BOURNE. 1964. Causes of mortality of the sea scallop (*Placopecten magellanicus*). *Proceedings of the National Shellfisheries Association*, Vol. 53, pp. 33–50.

POSGAY, J. A. 1957. Sea scallop boats and gear. *U.S. Fish and Wildlife Serv., Fishery Leaflet* No. 442, 11 pp.

PREMETZ, ERNEST D., AND GEORGE W. SNOW. 1953. Status of New England sea-scallop fishery. *Commercial Fisheries Review*, **15**(5): 1–17.

Appendix Tables follow.

APPENDIX TABLE I. Size frequency, in 5-mm groups, of scallops caught by 3-inch (76-mm) and 4-inch (102-mm) inside diameter ring scallop drags in October and November 1959.

	October		November		Total		Data equalized from 105 mm and over Correction factor = 1.234	
Shell height	3-inch	4-inch	3-inch	4-inch	3-inch	4-inch	3-inch	4-inch
mm								
25–29	1	...	...	...	1	...	1	...
30–34	...	...	...	...	...	...	...	...
35–39	4	3	...	1	4	4	5	4
40–44	5	1	4	2	9	3	11	3
45–49	4	2	5	6	9	8	11	8
50–54	20	14	26	20	46	34	57	34
55–59	32	15	59	56	91	71	112	71
60–64	52	26	46	49	98	75	121	75
65–69	43	32	15	21	58	53	72	53
70–74	34	14	7	7	41	21	51	21
75–79	16	5	14	4	30	9	37	9
80–84	16	9	47	32	63	41	77	41
85–89	49	41	161	121	210	162	259	162
90–94	129	96	394	309	523	405	645	405
95–99	286	278	525	491	811	769	1000	769
100–104	431	416	411	433	842	849	1039	849
105–109	310	362	323	366	633	728	781	728
110–114	123	183	232	275	355	458	438	458
115–119	72	128	171	217	243	345	300	345
120–124	72	83	80	102	152	185	188	185
125–129	45	53	42	31	87	84	107	84
130–134	14	34	15	23	29	57	36	57
135–139	16	15	7	7	23	22	28	22
140–144	8	7	5	4	13	11	16	11
145–149	3	6	1	1	4	7	5	7
150–154	1	3	...	...	1	3	1	3

APPENDIX TABLE II. Size frequency, in 5-mm groups, of scallops caught by 3-inch (76-mm) ring scallop drag with constant linkage (S/D), and scallops caught by 4-inch (102-mm) ring scallop drag when linked in four different ways. Data collected on Georges Bank, August–September 1961

Gear:	3-inch S/D vs. 4-inch S/D[a]		3-inch S/D vs. 4-inch D/D[b]		3-inch S/D vs. 4-inch D/T[c]		3-inch S/D vs. 4-inch D/Q[d]	
Shell height	Number of scallops		Number of scallops		Number of scallops		Number of scallops	
mm								
30–34	17	6	...	...	...	6	43	...
35–39	34	33	9	...	17	19	40	...
40–44	109	28	23	12	51	31	37	48
45–49	155	235	32	13	90	232	124	58
50–54	287	184	78	32	119	270	324	90
55–59	584	256	219	108	323	206	341	160
60–64	1,171	667	407	271	926	745	763	297
65–69	2,470	2,021	1,354	765	2,344	2,092	1,743	1,197
70–74	5,588	5,160	1,905	1,493	5,391	3,882	3,404	2,423
75–79	8,269	4,469	2,016	1,206	8,365	4,939	4,363	2,200
80–84	7,259	6,192	1,106	416	9,236	5,004	5,448	3,687
85–89	10,625	8,208	221	528	8,470	6,123	5,036	4,118
90–94	5,721	7,670	256	209	7,597	6,938	11,488	9,233
95–99	3,330	2,768	407	197	2,875	3,524	5,769	4,085
100–104	4,164	3,199	436	289	1,084	1,108	696	1,568
105–109	4,700	4,371	636	642	1,468	1,474	824	517
110–114	3,990	3,988	611	565	1,284	1,821	655	854
115–119	3,300	3,416	415	396	1,377	1,756	832	821
120–124	3,378	3,901	181	240	1,770	2,409	859	799
125–129	2,646	3,061	125	116	1,406	1,789	846	719
130–134	1,811	2,011	71	53	817	1,133	639	648
135–139	1,062	796	13	21	301	266	170	242
140–144	629	735	20	15	172	146	39	124
145–149	38	6	2	3	29	6	...	...

[a]S/D — rings in bag of drag joined by 1 link on top and 2 on bottom.
[b]D/D — rings in bag of drag joined by 2 links on top and 2 on bottom.
[c]D/T — rings in bag of drag joined by 2 links on top and 3 on bottom.
[d]D/Q — rings in bag of drag joined by 2 links on top and 4 on bottom.

APPENDIX TABLE III. Catch of discards (scallops under 100 mm), markets (scallops 100 mm and larger), scallops smaller than 95 mm, scallops 95–109 mm, and scallops 110 mm and larger, by 3-inch (76-mm) and 4-inch (102-mm) ring scallop drags, when the larger ring was linked in four different ways. Data collected on Georges Bank, August–September 1961.

	3-inch	4-inch	3-inch	4-inch	3-inch	4-inch	3-inch	4-inch	Totals	
Linkage:	S/D	S/D	S/D	D/D	S/D	D/T	S/D	D/Q	3-inch	4-inch
Number of tows:	19	19	3	3	12	12	5	5	39	39
Number of scallops less than 100 mm	45,619	37,897	8,033	5,250	45,804	34,011	38,923	27,596	138,379	104,754
Number of scallops 100 mm and larger	25,718	25,484	2,510	2,340	9,708	11,908	5,560	6,292	43,496	46,024
Percentage of scallops less than 100 mm	63.95	59.79	76.19	69.17	82.51	74.07	87.50	81.43	76.08	69.47
Percentage of scallops 100 mm and larger	36.05	40.21	23.81	30.83	17.49	25.93	12.50	18.47	23.92	30.53
Number of scallops less than 100 mm per tow	2,401	1,995	2,678	1,750	3,817	2,834	7,784	5,519	3,548	2,686
Number of scallops 100 mm and larger per tow	1,354	1,341	836	780	809	992	1,112	1,259	1,115	1,180
Number of scallops less than 95 mm	42,289	35,129	7,626	5,053	42,929	30,487	33,154	23,511	125,998	94,180
Number of scallops 95–109 mm	12,194	10,338	1,479	1,128	5,427	6,106	7,289	6,170	26,389	23,742
Number of scallops 110 mm and larger	16,854	17,914	1,438	1,409	7,156	9,326	4,040	4,270	29,488	32,919

Adjustment of Buoyancy in Young Atlantic Salmon and Brook Trout by Changes in Swimbladder Volume[1]

By Richard L. Saunders

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

The adjustment of swimbladder volume and the consequent effects on buoyancy in young Atlantic salmon and brook trout at various stages of development were measured in relation to current velocity. This was done by measuring pressure of neutral buoyancy — the pressure at which an anesthetized fish just reached neutral buoyancy as the total (atmospheric plus hydrostatic) pressure was gradually reduced — or by measuring flotation pressure — the ratio of volume of gas in the swimbladder to weight of the gas-free fish in water. Whether in static or flowing water, salmon parr were less buoyant than brook trout. Individuals of both species were more buoyant when held in still water than when held in rapidly flowing water. Adjustment in buoyancy took place when these fishes were subjected to a change in water current. Buoyancy was reduced if they were moved from still water to rapidly flowing water and was increased if they were moved from flowing to still water. Salmon smolts were more buoyant than salmon parr. This greater buoyancy of smolts is not owing to their being larger than parr. Initial filling of the swimbladder in salmon alevins can be delayed by subjecting them to strong water currents.

INTRODUCTION

An important function of the swimbladder in many fishes is that of a hydrostatic organ. By effecting changes in the swimbladder volume a fish changes its density. In still waters many fishes maintain densities close to that of the ambient water by adjusting swimbladder volume and thus require little or no expenditure of energy (swimming movements) to remain at a given depth. In flowing waters some species appear to reduce swimbladder volume and achieve densities greater than that of their environment. Thus a fish may be spoken of as being in positive, negative, or neutral buoyancy depending on whether it rises, sinks, or remains at a given depth in the absence of any swimming movements. It may be reasonably assumed that a fish in negative buoyancy can more easily maintain a position on the bottom of a swift stream and resist being swept downstream than one in neutral or positive buoyancy.

Hora (1922) shows that there is a distinct relation between swimbladder volume and the intensity of current in which a number of Indian cyprinid fishes live. Individuals from swifter streams have reduced swimbladders in comparison with those from quieter water. Swimbladder volume appears to be related to environment and is not necessarily a specific character. Hora (1921) reports that within a species of the genus *Garra* there is variation in swimbladder volume in adults but that the swimbladders in young individuals are alike and of the normal form.

[1]Received for publication August 21, 1964.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

Gee and Northcote (1963) showed in a field-laboratory study with two sympatric species, leopard dace (*Rhinichthys falcatus*) and longnose dace (*R. cataractae*), that the swimbladder volumes of the two species are similar in fry as are their habitats and food. As these species grow, their swimbladder volumes as well as habitat preferences change. Bladder volumes of leopard dace increase with fish size and these fish show a preference for quiet water. Bladder volumes of longnose dace increase little as the fish grow and these fish show a decided preference for flowing water.

Atlantic salmon may have different degrees of distension of the swimbladder and this depends on the type of habitat in which they live. White (personal communication) found that parr from slowly flowing or still water had well-filled swimbladders while those from rapids had little gas in their swimbladders. The objective of the present work was to study the adjustments in buoyancy in young Atlantic salmon and brook trout under various conditions of current and at various stages of development.

MATERIALS AND METHODS

Salmon parr and smolts (*Salmo salar*) and brook trout (*Salvelinus fontinalis*) used for determinations of pressure of neutral buoyancy were wild fish from the Northwest Miramichi River, N.B. Salmon alevins (sac fry) and fry were from the Miramichi Fish Culture Station, N.B. Brook trout and salmon parr and smolts used for determinations of flotation pressure were from the Saint John Fish Culture Station, N. B.

Pressure of Neutral Buoyancy

The technique used to measure buoyancy of fish is an application of the Cartesian diver principle as used by Brown (1939) and Tait (MS, 1959). In this case an anesthetized fish is the diver. The swimbladder volume and hence the density of the fish can be changed by varying the pressure. Fish were held in a container (a large carboy or a flume described below) which could be made air-tight. A partial vacuum was applied in the container and the reduction in pressure measured with a mercury manometer. Pressure was reduced until the anesthetized fish just rose off the bottom of the container. The atmospheric pressure minus the reduction in pressure necessary to float the fish gives a value herein referred to as pressure of neutral buoyancy. No correction is made for depth of water because the hydrostatic pressure resulting from a water depth of 10 cm is only about one-hundredth of an atmosphere. For comparison among fish in this work, buoyancy increases as pressures of neutral buoyancy rise towards atmospheric pressure.

In the field some measurements were made for wild salmon parr and brook trout. These fish had been held for various periods in two screened cages in the river. One cage was placed in mid stream in a heavy current which was no less than 46 cm/sec during low water and much greater during freshets. The other cage was near shore in a sheltered area where the current was sufficient to renew

the water but make no appreciable movement through the cage. A 6-inch layer of stones ranging in size from 1 to 4 inches covered the bottom of each cage. These anchored the cages and provided hiding places for the fish. Except for organisms which may have passed through the $\frac{1}{2}$-inch mesh of the cages, fish were unfed during experiments.

Fish were captured individually from the cages by dip net, taken ashore, and placed in a 13-liter carboy filled with water to a depth of 10 cm (Fig. 1). They were anesthetized with tricane methanesulfonate (M.S. 222). A portable, electric vacuum pump was used to reduce the pressure in the carboy. After the pressure of neutral buoyancy had been measured, fish were allowed to resume swimming and respiratory movements and were then returned to their respective cages.

In the laboratory, fish were held prior to experiments in the containers in which measurements were to be made to preclude handling and possibly forcing gas from the swimbladder. Salmon alevins and fry were held in 13-liter glass carboys in which circular currents of various speeds were produced by directing the water inflow around the inner periphery of the carboy (Fig. 2). The outlet was a screened tube with its opening at the center about 2 inches from the bottom. Inlet and outlet tubes passed through a rubber stopper in the opening of the carboy. A third tube through the stopper was used for applying a vacuum but was clamped off except during measurements. The inlet-outlet arrangement ensured a constant depth of water in the carboy. As water entered the system and filled the carboy slightly above the opening of the outlet tube, a slight positive air pressure was built up in the carboy, causing water to rise in the outlet tube and to flow out of the system. A screw clamp was used on the inlet tube to maintain a constant flow.

Experiments with parr and smolts were done in a flume (Fig. 3). This was a plexiglass trough 122 cm long in which currents of various speeds were maintained by a submersible electric pump, outside the trough, which drew water

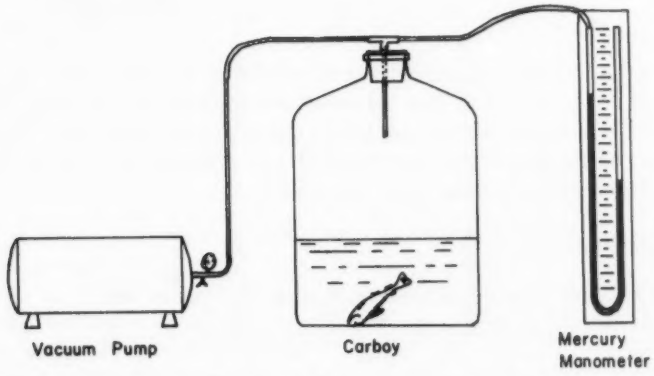


FIG. 1. Cartesian diver apparatus for measuring pressure of neutral buoyancy.

from one end of the trough and forced it in the other. The flume, submersible pump, and associated piping were held in a constant temperature bath provided with flowing water. The pump was fitted with a rheostat for controlling its output and hence the rate of flow through the flume. Rates of flow up to 26 cm/sec could be maintained for many days and fish once placed in the apparatus did not need to be disturbed by handling. Fish were held in a 50 cm long section of the trough screened at either end and covered at the top. At the inlet end of the flume there was a plexiglass baffle slanting downwards to the front screen from a point 13 cm from the inlets. This baffle shielded the screened section from jets of water from the inlets and allowed a smooth flow down its slanting surface and through the screened section. During measurements of neutral buoyancy the screens were replaced with plexiglass doors which were fitted with rubber

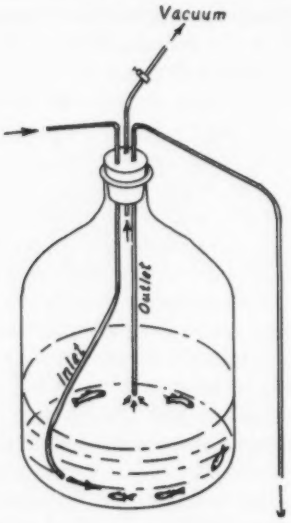


FIG. 2. Apparatus for holding fish in water of constant current velocity.

gaskets. A vacuum line was attached to a tube in the then air-tight or pneumatic section of the flume. The fish were anesthetized by injecting a solution of M.S. 222 into the fluvarium just before the doors were inserted. The pressure inside the pneumatic section was reduced and pressures of neutral buoyancy were measured in the manner described above.

FLOTATION PRESSURE

Whereas the pressure of neutral buoyancy may be taken as an indirect measure of swimbladder volume, the flotation pressure is derived from direct measurement of swimbladder volume (Saunders, 1953). Flotation pressures were measured for hatchery-reared salmon and trout which had been held in still water for various periods. The method consists of cutting a fish open

under water, collecting and measuring the volume of released swimbladder gas in an inverted, water-filled burette and then weighing the gas-free fish under water. The volume of gas (in milliliters) divided by the weight (in grams) of the gas-free fish in water gives the flotation pressure. A quotient of 1 ml/g would indicate that the fish was in neutral buoyancy at atmospheric pressure. Fractional values would indicate that pressures of neutral buoyancy are less than atmospheric.

RESULTS

Effects of Current Velocity on Buoyancy of Salmon and Trout

Eight sets of field measurements of pressures of neutral buoyancy were made for salmon and four sets for trout after the fish had been held for various periods in their respective cages in flowing (approximately 46 cm/sec) and still water. The results are shown in Fig. 4. Salmon parr only were used in experiment 1. These were left for 26 days before measurements were made and for an additional 16 days before a second set of measurements was made. Salmon parr and trout were used together in experiment 2 where initial measurements were made sooner and subsequent ones were made at more frequent intervals.

Mean pressures of neutral buoyancy for salmon and trout were consistently higher in fish from still water than in those from flowing water. In experi-

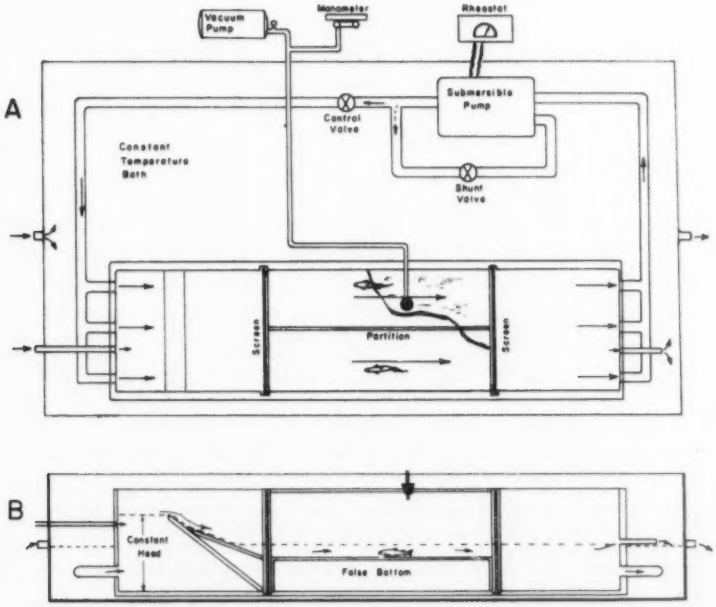


Fig. 3. Flume for holding fish in various constant current velocities and in which pressure of neutral buoyancy can be measured without handling fish. A — top view, B — side view.

ment 1, pressures of neutral buoyancy were higher for both fast- and slow-water groups than for corresponding groups of salmon in experiment 2 where measurements were made sooner. Following the measurements on day 13 (experiment 2), the salmon and trout from the slow-water cage were put in the fast-water cage and vice versa. Fourteen hours after the reciprocal change, buoyancy in each group had been adjusted to the new current conditions. There was no further change in buoyancy 36 hr after the transposition.

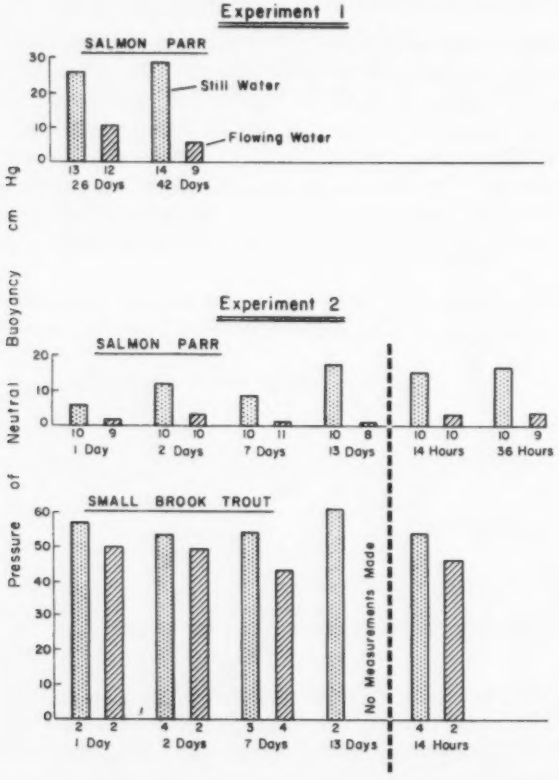

Experiment 1
SALMON PARR
Still Water
Flowing Water
13 12 14 9
26 Days 42 Days
Experiment 2
SALMON PARR
10 9 10 10 10 11 10 8 10 10 10 9
1 Day 2 Days 7 Days 13 Days 14 Hours 36 Hours
SMALL BROOK TROUT
2 2 4 2 3 4 2 4 2
1 Day 2 Days 7 Days 13 Days 14 Hours
No Measurements Made
Pressure of Neutral Buoyancy cm Hg

FIG. 4. Pressures of neutral buoyancy for salmon parr and small brook trout from flowing and still water. *Experiment 1*: One group of large salmon parr (about 10 cm) held in cage in flowing water (approximately 46 cm/sec) and other group in cage in still water. Buoyancies measured after 26 and 42 days. *Experiment 2*: Salmon parr and brook trout held together in cages in flowing and still water. Buoyancies measured at various intervals up to 13 days. Then fish transposed from one cage to the other and buoyancies measured again after 14 and 36 hr. Numbers of fish involved and time they spent in respective cages indicated below each pair of bars. Each bar represents mean pressure of neutral buoyancy.

Pressures of neutral buoyancy for brook trout from both still and flowing water were much higher than corresponding values for salmon parr. Moreover, they approached atmospheric pressure (76 cm Hg). Although salmon parr from still water were more buoyant than those from flowing water, neither group approached neutral buoyancy at atmospheric pressure.

Smolts More Buoyant Than Parr

Pressures of neutral buoyancy were measured in 22 laboratory experiments in each of which a smolt and a parr were paired in the flume. The results are given in Table I and Appendix I. In 17 tests smolts were more buoyant than parr and in the remainder neither fish floated at the maximum reduction in pressure of which the apparatus was capable. On the average, the smolts had a pressure of neutral buoyancy of 33.6 cm Hg or slightly less than half an atmosphere, while that for parr was 14.7 cm Hg or about one-fifth of an atmosphere. The distributions of pressures of neutral buoyancy of smolts and parr were analyzed using the Kolmogorov-Smirnov test (Siegel, 1956) and were found to be significantly different at the P = 95% level.

Table I. Pressures of neutral buoyancy of smolt and parr.

Smolt or parr — number	Mean size (range)		Mean pressure of neutral buoyancy (range) (*cm Hg*)
	Weight (g)	Length (*cm*)	
Smolts 22	26.4(17.1–36.8)	14.7(13.1–15.7)	33.6 (<1.0–70.2)
Parr 22	10.9(4.6–14.8)	10.3(7.8–11.5)	14.7 (<1.0–51.3)

The above measurements were made after the various parr-smolt pairs had been held in different current conditions. Within experiments current was held at some constant level; among experiments it ranged from 0 to 25.4 cm/sec. There was no apparent correlation between current speed and pressure of neutral buoyancy, perhaps because data are too few and the current speeds are not diverse enough. Consequently, current speed is not discussed further.

The smolts were consistently larger than the parr but the length of fish (length class) did not seem to affect buoyancy. The disposition of fish in different classes with respect to buoyancy and length does not differ significantly from a random one. To establish whether or not fish size was responsible for the observed differences in buoyancy between parr and smolts, 11 experiments were conducted in which a large and a small parr were paired in each. Mean lengths of the large and small parr were 13.6 and 9.2 cm, respectively. Each experiment was done under constant current conditions. Among experiments currents ranged from 0 to 25.4 cm/sec. The results are given in Table II and Appendix II. Pressures of neutral buoyancy were very low in both groups.

TABLE II. Pressures of neutral buoyancy of large and small parr.

Large or small — number	Mean size (range)		Mean pressure of neutral buoyancy (range) (*cm Hg*)
	Weight (*g*)	Length (*cm*)	
Large 11	26.2(21.8–31.8)	13.6(12.8–14.2)	1.4 (<1.0–2.1)
Small 11	8.2(4.1–10.1)	9.2(7.5–9.9)	5.2 (<1.1–29.7)

Although the means differ, the distributions were found by the Kolmogorov-Smirnov test not to differ significantly at the P = 95% level. There is no evidence that greater size of smolts is responsible for the observed greater buoyancy of smolts than of parr.

FLOTATION PRESSURES OF SALMON PARR AND SMALL BROOK TROUT

In order to provide direct measurements of swimbladder volume and to relate these to pressures of neutral buoyancy, a limited series of flotation pressures was determined in December for salmon parr and small brook trout held in the laboratory. The results are summarized in Table III and Appendix III. The distributions of flotation pressures of salmon parr and small brook trout were found by the Kolmogorov-Smirnov test to differ significantly at the P = 95% level. The mean flotation pressure for trout is 0.84 ml/g. This corresponds with a pressure of neutral buoyancy of 68 cm Hg which is of the same order of magnitude as those shown for trout in Fig. 4. The mean flotation pressure for the salmon parr is 0.43 ml/g. This corresponds with a pressure of neutral buoyancy of 33 cm Hg which is higher than those for salmon parr in Fig. 4.

A second series of flotation pressure measurements was made in April at which time some smolts were available. These data for parr, smolts, and trout are summarized in Table IV and Appendix IV. Mean flotation pressures and the corresponding pressures of neutral buoyancy are 0.42 ml/g (32 cm Hg) for

TABLE III. Flotation pressures of salmon parr and trout from still water.

Salmon or trout — number	Mean length (range) (*cm*)	Mean swimbladder volume at atmospheric pressure (range) (*ml*)	Mean weight of fish in water (range) (*g*)	Mean flotation pressure (range) (*ml/g*)	Corresponding mean pressure of neutral buoyancy (*cm Hg*)
Salmon 14	10.2(8.9–11.3)	0.26(0–0.6)	0.59(0.4–0.8)	0.43(0–0.9)	33
Trout 34	12.6(9.3–17.0)	0.96(0.4–2.28)	1.15(0.5–3.0)	0.84(0.5–1.0)	68

TABLE IV. Flotation pressures of salmon parr and smolts and brook trout from still water.

Salmon parr, smolts or trout — number	Mean length (range) (*cm*)	Mean swimbladder volume at atmospheric pressure (range) (*ml*)	Mean weight of fish in water (range) (g)	Mean flotation pressure (range) (*ml/g*)	Corresponding mean pressure of neutral buoyancy (*cm Hg*)
Parr 10	9.6(8.4–10.5)	0.23(0.1–0.35)	0.53(0.4–0.7)	0.42(0.25–0.88)	32
Smolts 10	12.9(11.9–14.2)	0.85(0.45–1.20)	1.17(0.9–1.4)	0.71(0.50–0.85)	54
Trout 10	13.1(11.7–15.9)	1.25(0.65–2.45)	1.36(0.8–2.3)	0.93(0.72–1.22)	71

parr, 0.71 ml/g (62 cm Hg) for smolts, and 0.93 ml/g (71 cm Hg) for trout. There was little difference in the values for parr in December and April. The smolts and parr were held together in one tank and were distinguished on the basis of coloration. Those having silvery scales and black pigmentation of the caudal and pectoral fins were considered to be smolts whereas those with silvery scales but no black color of the fins were considered to be parr. The average flotation pressure for smolts was nearly twice as high as that for parr. Trout had flotation pressures over twice as high as those of parr but only about 30% higher than those of smolts.

The distributions of flotation pressures among parr, smolts, and trout were analysed using the Kolmogorov-Smirnov test. Parr–trout differences were significant at the P = 95% level. Parr–smolt differences were slightly less than significant. There was not a significant difference in distribution of flotation pressures between smolts and trout.

INITIAL FILLING OF SWIMBLADDER AFFECTED BY CURRENT

Salmon alevins which had been hatched about April 12 were placed on May 30 in a fiberglass tank in which they had free access to the water surface. At this stage the alevins still had large yolk sacs and remained on the bottom. On June 12, 20 alevins were placed in each of two 13-liter carboys filled with water to a depth of 8 cm and in which there were circular currents. One carboy had a current of about 1 cm/sec and the other about 8.7 cm/sec. Current velocities were maintained close to these values and the swimming behavior of the alevins was observed during the next 3 weeks. Alevins remaining in the fiberglass tank served as controls.

The fish in the carboy with a slow current faced the current but rested on the bottom and swam only occasionally. Those in the fast current had to swim steadily and vigorously to avoid being swept around the carboy. These alevins were able to stem the current for many days. Regular feeding with ground beef liver was started on June 13 because yolk sacs were nearly depleted. On June 14 some of the alevins in the open tank and in the carboy with slow current were

observed swimming near the surface. However, they swam with difficulty and sank when swimming movements stopped. One swimmer from the open tank was examined and had no gas in the swimbladder.

During the next 4 days the alevins in the carboy with slow current and in the open tank continued to swim about off the bottom but sank when they stopped swimming. Those in the fast current were still able to maintain position against the current. On June 19, two fish in the slow water and many in the open tank were obviously buoyant; they swam off the bottom and did not sink quickly when they stopped swimming. Two of the latter were examined with a dissecting microscope and the swimbladders were distended with gas. The alevins at this time were about 3 cm long. On June 21 an alevin was observed gulping air at the surface. By June 22 most of the fish in the slowly flowing water and in the open tank had filled their swimbladders and were swimming easily in mid water. None of those in the carboy with rapidly flowing water showed signs of buoyancy until June 25. Sometime during the previous night a dead fish clogged the outlet and reduced the flow almost to nil. On the morning of June 25 some of the fish were obviously buoyant and when the flow was re-established these drifted around with the current and appeared unable to sound and maintain positions on the bottom of the carboy as nonbuoyant individuals were doing.

DISCUSSION

Negative Buoyancy an Advantage in Swift Streams

Results of previous work have emphasized the importance of the swimbladder as a hydrostatic organ which helps a fish in a stillwater environment to maintain a position off the substrate with little expenditure of energy. This is accomplished by adjustments in swimbladder content such that the fish has a density near that of water. The present results indicate that the stream-dwelling young of Atlantic salmon maintain low swimbladder volumes and consequent high densities. Were they to do otherwise, their buoyancy would be increased and it would be difficult for them to stay near the bottom and resist being swept downstream by the current. This was clearly illustrated in the experiments wherein fry with recently filled swimbladders were unable to stay on the bottom and resist being swept around the container. Like other physostomes studied, salmon appear to have a strong tendency to initiate filling of their swimbladders soon after their yolk sacs are absorbed. However, they apparently do not do so when the resulting increased buoyancy would be to their disadvantage as in a strong current. Tait (MS, 1960) demonstrated that if swimbladder filling in brown trout, rainbow trout, lake trout, and whitefish is experimentally delayed by barring their access to the surface, these species do not lose the ability to fill their swimbladders later and that they fill them at the first opportunity. In the present study the maintenance of a swift current (but with access to the surface) resulted in a short delay in filling until an accident stopped the current. Salmon in streams are likely able to delay initial swimbladder filling until the current is gentle or they have moved to the stream

margin. Their ability to maintain position against the current as demonstrated in these experiments may allow alevins, newly emerged from the gravel, to swim far enough to reach quiet waters near shore or rough-bottomed areas which provide protection from the current.

Kalleberg (1958) observed that if salmon alevins in an experimental stream tank swim to the surface to fill their swimbladders they are displaced downstream. Since no such displacement occurred in his experiments but many fish were found to have filled swimbladders, he concluded that these filled their bladders by catching bubbles which are swept along below the surface of the stream. In the present work, alevins were observed to take bubbles which were swept around the carboy. However, such bubbles were usually rejected and the fish did not become buoyant until the current was accidentally stopped. Kalleberg's observations in a stream tank with a gravel bottom were made under conditions closer to nature than those reported here. However, the present observations do emphasize that swimbladder filling and the consequent increase in buoyancy can be delayed.

White (personal communication) found that in salmon parr of any size the swimbladder might have no distension or it might be well developed and filled with gas. He found that parr from slowly flowing or still water invariably had well-filled swimbladders whereas those in fish from rapidly flowing sections were empty. It was established in the present work that parr reduce their swimbladder volumes after they have been moved from still to flowing water and the reverse. This appears to be an adaptive mechanism whereby young salmon adjust their density such that those in flowing water have reduced buoyancy making it easier for them to maintain position on or near the bottom, whereas those in pools have greater buoyancy making it easier for them to swim in mid water. Atlantic salmon parr are known to move from pools to riffles or vice versa (Saunders and Gee, 1964) and may have to adjust their buoyancies to meet the changing conditions.

Time for Adjustment to Changing Current Speed

One aspect of buoyancy regulation which needs more attention is the time required for adjustment of swimbladder volume after the fish have been subjected to a change in current velocity. Some preliminary observations during this study indicate that the adjustment is made within 46 hr in fry and less than 14 hr in large parr. From the point of view of fish cultural practices of planting hatchery-reared salmon of various sizes in streams, it is important to learn how quickly the fish meet an abrupt change in current speed by adjusting swimbladder volume.

Significance of Increased Buoyancy of Smolts

The observed greater buoyancy of smolts as compared with parr probably has biological significance when it is considered that smoltification represents a special adaptation during which an essentially bottom-living fish — the parr —

prepares as a smolt for a pelagic mode of life in the sea. Evropeitseva (1959) reports that smolts display greater activity and swim mainly at mid depth during the process of smoltification. It is interesting that during the process of smoltification the fat content is sharply reduced (Lovern, 1934; Malikova, 1957). Lovern reports that the fat content of a group of parr was 3.9% while that of smolts was only 1.2% and further that the fat of smolts is more like that of marine fish in respect to the types of fatty acids found in it than that of freshwater fish. He suggests that the smolt is in a transitional stage, in regard to its fat, between the freshwater and saltwater stages and that the reduced fat content of smolts suggests a partial withdrawal of fat to effect the change. In respect to the present observations, the greater buoyancy of smolts than parr is even more striking when it is realized that the increase in buoyancy is in spite of a decrease in fat content. Such a decrease would tend to increase the fish's density.

A condition of increased buoyancy is very likely involved in the downstream migration of smolts. Huntsman (1962) maintains that smolts are less vigorous than fat parr and that this lack of vigor together with their tendency to keep away fron the bottom "... results in their not reacting sufficiently to current by heading and swimming upstream for them to continue as river fish." Kalleberg (1958) observed that smolts in a circular channel schooled and swam day and night with the current. Whether the seaward movement of smolts is by active swimming downstream or by random movements with the net movement being downstream, such downstream movement must be enhanced by increased buoyancy.

Salmon Parr Less Buoyant Than Brook Trout

The differences in buoyancy between young salmon and brook trout are probably indicative of their different ecology. When salmon parr and brook trout occur together in the same stream, the salmon are most often found in the rapidly flowing water and the trout in the pools or more slowly flowing water. If trout occur in a section of river which is mainly fast water, they are most likely to be found along the stream margin or near boulders where there are places of low current velocity. A logical conclusion is that salmon parr by virtue of their ability to reduce their buoyancy are adapted for living in rapid currents and that the more buoyant brook trout are less well adapted for living in rapids. Both species show plasticity in respect to buoyancy. Each can adjust to changes in current, the salmon apparently having the greater latitude for adjustment. This thinking is supported by the observations of J. W. Saunders (personal communication) who found in a stream on Prince Edward Island that during years with low population densities of brook trout, salmon parr were found in both riffles and pools, but in years when trout were abundant, salmon parr were found principally in riffles.

SUMMARY

The adjustment of buoyancy in young Atlantic salmon and brook trout was studied by measuring the pressure of neutral buoyancy and the flotation

pressure. The former measurement is made by subjecting an anesthetized fish to gradually reduced pressures until it just reaches neutral buoyancy. Flotation pressure is derived by dividing the volume of swimbladder gas measured at atmospheric pressure by the weight of the gas-free fish in water.

1. All salmon parr studied were in negative buoyancy. Those from rapidly flowing water were less buoyant than those from still water.
2. Brook trout were more buoyant than salmon parr. Trout from still water were more buoyant than those from flowing water and occasionally approached neutral buoyancy.
3. Salmon smolts were more buoyant than parr. This greater buoyancy was not owing to the larger size of smolts in comparison with parr.
4. Flotation pressures of small brook trout were higher than those of salmon parr. Whereas flotation pressures of trout were often near 1.0 indicating neutral buoyancy, those of salmon parr were mostly low indicating pronounced negative buoyancy. Flotation pressures of smolts were nearly as high as those of brook trout.
5. Initial filling of the swimbladder in salmon alevins can be delayed by subjecting the fish to strong water currents.

ACKNOWLEDGMENTS

I am grateful to summer assistant, Miss Nancy Peters (Mrs David Neave), who showed a keen interest in this work and carried out many of the laboratory experiments. Mr Eugene Henderson assisted with the measurements of flotation pressure. I thank our field technicians and summer assistants of the Anadromous Fish Investigation who collected wild fish and assisted with the field experiments.

I am grateful to Mr Joe Johnson who carefully made the experimental flume and to Mr Hill Brownrigg who contributed his ideas for making this useful piece of apparatus.

Dr Paul F. Elson offered helpful suggestions for this research and for preparation of the manuscript. Drs John L. Hart and Morden W. Smith and Messrs J. Wilfred Saunders, Jyri Paloheimo and Emygdio Cadima offered helpful suggestions for presentation of data and improvement of the manuscript.

REFERENCES

Brown, F.A., Jr. 1939. Responses of the swimbladder of the guppy, *Lebistes reticulatus*, to sudden pressure decreases. *Biol. Bull.*, **76**(1): 48–58.

Evropeitseva, N.V. 1959. Transformation to smolt stage and downstream migration of young salmon. *Uchenye Zapiski Leningradskogo Gosud. Univ.* (*LGU*), No. 228, *Ser. Biol. Nauk* No. 44, pp. 117–154. [Fish. Res. Bd. Canada, Translation Series No. 234.]

Gee, J.H., and T.G. Northcote. 1963. Comparative ecology of two sympatric species of dace (*Rhinichthys*) in the Fraser River system, British Columbia. *J. Fish. Res. Bd. Canada*, **20**(1): 105–118.

HORA, S.L. 1921. XXIX. Indian cyprinoid fishes belonging to the Genus *Garra*, with notes on related species from other countries. *Records of the Indian Museum*, **22**: 633–688.
1922. The modification of the swimbladder in hill stream fishes. *J. Asiatic Soc. Beng.*, **18**: 5–7.

HUNTSMAN, A.G. 1962. Method in ecology — Ectology. *Ecology*, **43**(3): 552–556.

KALLEBERG, H. 1958. Observations in a stream tank of territoriality and competition in juvenile salmon and trout (*Salmo salar* L. and *S. trutta* L.). *Fish. Bd. Sweden, Inst. Freshwater Res. Drottningholm, Rept.* No. 39, pp. 55–98.

LOVERN, J.A. 1934. Fat metabolism in fishes. V. The fat in the salmon in its young freshwater stages. *Biochem. J.*, **28**(2): 1961–1963.

MALIKOVA, E.M. 1957. Biochemical analysis of young salmon at the time of their transformation to a condition close to the smolt stage, and during retention of smolts in fresh water. *Trudy Latviiskogo Otdel. VNIRO*, **2**: 241–255. [Fish. Res. Bd. Canada, Translation Series No. 232.]

SAUNDERS, R.L. 1953. The swimbladder gas content of some freshwater fish with particular reference to the physostomes. *Canadian J. Zool.*, **31**(6): 547–560.

SAUNDERS, R.L., AND J.H. GEE. 1964. Movements of young Atlantic salmon in a small stream. *J. Fish. Res. Bd. Canada*, **21**(1): 27–36.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill Book Company, New York, pp. 127–136.

TAIT, J. S. MS, 1959. Swimbladder studies in salmonoids relating to problems of depth. PhD. Thesis, Dept. of Zool., Univ. of Toronto.
1960. The first filling of the swimbladder in salmonoids. *Canadian J. Zool.*, **38**: 179–187.

APPENDIX I. Pressures of neutral buoyancy of smolt and parr.

Date	Smolt or parr	Size		Current velocity (*cm/sec*)	Pressure of neutral buoyancy (*cm Hg*)
		Weight (g)	Length (*cm*)		
5/6/62	s	17.1	13.1	12.2	68.4
5/6/62	p	4.6	7.8	12.2	26.9
6/6/62	s	21.0	13.5	12.2	25.8
6/6/62	p	14.5	11.5	12.2	35.8
6/6/62	s	19.0	13.1	12.2	28.8
6/6/62	p	14.1	11.2	12.2	13.8
7/6/62	s	25.0	14.5	10.7	36.8
7/6/62	p	14.8	11.1	10.7	32.3
7/6/62	s	24.2	14.4	12.2	51.8
7/6/62	p	12.1	10.6	12.2	< 1.0
8/6/62	s	27.4	15.0	11.4	42.9
8/6/62	p	13.5	11.1	11.4	16.9
8/6/62	s	32.5	15.7	12.2	61.9
8/6/62	p	10.5	9.8	12.2	36.9
9/6/62	s	33.6	15.6	11.2	34.8
9/6/62	p	9.2	9.8	11.2	14.8
11/6/62	s	26.5	14.9	12.2	< 1.0
11/6/62	p	12.3	10.8	12.2	< 1.0
12/6/62	s	28.8	15.1	12.7	28.1
12/6/62	p	13.9	10.9	12.7	3.1
12/6/62	s	36.8	17.2	12.2	41.6
12/6/62	p	12.2	11.3	12.2	16.6
13/6/62	s	31.0	15.2	0.8	70.2
13/6/62	p	8.8	9.8	0.8	29.8
13/6/62	s	28.2	14.8	14.0	< 1.0
13/6/62	p	6.3	8.7	14.0	< 1.0
17/6/62	s	25.6	14.7	13.5	61.5
17/6/62	p	8.8	9.8	13.5	51.3
21/6/62	s	29.0	15.3	1.1	48.7
21/6/62	p	14.1	10.9	1.1	16.1
21/6/62	s	24.6	14.4	14.0	< 1.0
21/6/62	p	13.2	11.0	14.0	< 1.0
22/6/62	s	29.6	15.3	8.9	64.2
22/6/62	p	7.9	8.9	8.9	< 1.2
25/6/62	s	28.3	15.1	9.7	< 1.0
25/6/62	p	14.0	11.0	9.7	< 1.0
25/6/62	s	23.7	14.2	19.1	12.2
25/6/62	p	10.2	10.2	19.1	< 1.0
26/6/62	s	26.5	14.8	12.7	14.0
26/6/62	p	7.0	11.2	12.7	< 1.0
27/6/62	s	20.1	13.6	9.2	43.5
27/6/62	p	7.8	9.0	9.2	19.3
27/6/62	s	24.1	13.9	25.3	< 1.0
27/6/62	p	10.8	9.8	25.3	< 1.0
Means:	s	26.4	14.7	–	33.6
	p	10.9	10.3	–	14.7

APPENDIX II. Pressures of neutral buoyancy of large and small parr.

Date	Large or small parr	Size		Current velocity (*cm/sec*)	Pressure of neutral buoyancy (*cm Hg*)
		Weight (g)	Length (*cm*)		
14/8/62[a]	L	27.0	14.0	12.2	< 2.1
14/8/62	S	9.7	9.9	12.2	< 2.1
14/8/62[b]	L	31.8	14.2	0	< 2.1
14/8/62	S	10.1	9.7	0	< 2.1
15/8/62[a]	L	27.0	14.0	0	< 1.1
15/8/62	S	9.7	9.9	0	< 1.1
15/8/62[b]	L	31.8	14.2	12.2	< 1.1
15/8/62	S	10.1	9.7	12.2	< 1.1
16/8/62[a]	L	27.0	14.0	0	< 1.2
16/8/62	S	9.7	9.9	0	< 1.2
16/8/62[b]	L	31.8	14.2	12.2	< 1.2
16/8/62	S	10.1	9.7	12.2	3.2
19/8/62[c]	L	22.9	13.1	25.4	< 1.2
19/8/62	S	7.8	9.2	25.4	13.2
20/8/62[c]	L	22.9	13.1	0	< 1.7
20/8/62	S	7.8	9.2	0	29.7
22/8/62[d]	L	21.8	12.8	23.2	< 1.2
22/8/62	S	5.5	8.2	23.2	< 1.2
23/8/62[d]	L	21.8	12.8	0	< 1.0
23/8/62	S	5.5	8.2	0	1.2
23/8/62	L	22.2	12.9	24.1	< 1.0
23/8/62	S	4.1	7.5	24.1	1.2
Means:	L	26.2	13.6	–	1.4
	S	8.2	9.2	–	5.2

[abcd] = same pairs of fish used for determinations on 3, 3, 2, 2 days, respectively.

APPENDIX III. Winter measurements of flotation pressures of salmon parr and trout from still water. Determinations made January 17. Water temperature 5°C.

	Length (*cm*)	Swimbladder volume at atmospheric pressure (*ml*)	Weight of fish in water (g)	Flotation pressure: swimbladder volume (*ml*) / weight in water (g)
Salmon parr				
	11.1	0.55	0.79	0.70
	10.5	0.56	0.62	0.90
	11.2	0.45	0.79	0.57
	10.5	0.10	0.60	0.17
	10.3	0.25	0.61	0.41
	10.3	0.30	0.53	0.57
	10.4	0.20	0.60	0.33
	10.5	0.07	0.69	0.10
	9.6	0.30	0.50	0.60
	9.2	0.30	0.43	0.70
	9.0	0.15	0.40	0.37
	8.9	0	0.35	0
	11.3	0.10	0.80	0.12
	9.8	0.28	0.51	0.55
Means:	10.2	0.26	0.59	0.43
Trout				
	13.3	0.90	1.30	0.69
	13.8	1.17	1.41	0.83
	13.5	0.96	1.13	0.85
	14.4	1.23	1.88	0.65
	14.2	1.50	1.68	0.89
	17.0	2.28	2.99	0.76
	14.4	1.40	1.62	0.86
	12.6	0.93	1.07	0.87
	14.3	1.60	1.78	0.90
	14.7	1.73	1.70	1.02
	13.5	0.70	1.41	0.50
	10.7	0.50	0.62	0.81
	13.4	1.30	1.33	0.98
	14.0	1.10	1.33	0.83
	12.9	0.84	1.07	0.78
	12.0	0.85	0.90	0.94
	11.4	0.72	0.80	0.90
	11.8	0.80	0.88	0.91
	13.1	1.28	1.34	0.95
	12.8	0.75	1.10	0.68
	12.9	0.87	1.19	0.73
	11.9	0.64	0.88	0.73
	12.6	0.90	1.02	0.88
	10.3	0.54	0.62	0.87
	11.4	0.65	0.80	0.81
	12.0	1.00	0.99	1.01
	10.8	0.70	0.70	1.00
	11.0	0.75	0.71	1.06
	11.4	0.57	0.78	0.73
	11.3	0.54	0.70	0.77
	10.7	0.40	0.64	0.62
	11.3	0.70	0.71	0.99
	9.3	0.45	0.50	0.90
	14.0	1.25	1.44	0.87
Means :	12.6	0.96	1.15	0.84

APPENDIX IV. Spring measurements of flotation pressures of salmon parr and smolts and brook trout from still water. Determinations made April 21. Water temperature 6°C.

	Length (*cm*)	Swimbladder volume at atmospheric pressure (*ml*)	Weight of fish in water (*g*)	Flotation pressure: swimbladder volume (*ml*) / weight in water (*g*)
Parr				
	10.5	0.20	0.7	0.29
	9.8	0.15	0.6	0.25
	9.6	0.30	0.4	0.75
	10.3	0.15	0.6	0.25
	9.0	0.20	0.4	0.50
	9.5	0.20	0.6	0.33
	9.3	0.15	0.6	0.25
	8.4	0.10	0.4	0.25
	9.2	0.35	0.4	0.88
	10.0	0.30	0.6	0.50
Means:	9.6	0.23	0.53	0.42
Smolts				
	12.5	0.70	1.1	0.64
	12.6	0.90	1.1	0.82
	13.6	1.10	1.4	0.79
	13.5	1.10	1.3	0.85
	12.5	0.60	1.2	0.50
	11.9	0.65	0.9	0.72
	13.0	0.90	1.2	0.75
	14.2	1.20	1.5	0.80
	12.7	0.85	1.1	0.77
	12.3	0.45	0.9	0.50
Means:	12.9	0.85	1.17	0.71
Trout				
	14.5	1.30	1.7	0.76
	10.5	0.90	0.8	1.12
	15.8	1.85	2.3	0.80
	15.9	2.45	2.0	1.22
	13.4	1.30	1.5	0.87
	10.4	0.70	0.8	0.87
	11.8	0.65	0.9	0.72
	13.3	1.20	1.0	1.20
	11.7	0.85	0.9	0.94
	14.0	1.35	1.7	0.79
Means:	13.1	1.25	1.36	0.93

Drift Bottle Observations in Northumberland Strait, Gulf of St. Lawrence[1]

By L. M. Lauzier

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

Drift bottles have been released at fixed stations and during cruises in Northumberland Strait from 1960 to 1963. From the 2741 releases, there have been 1213 recoveries before the winter seasons. The overall high percentage recovery (44%) and the large number of returns not far from the point of release and within a short time after releases are featured.

The drift bottle recoveries suggest a surface non-tidal drift through Northumberland Strait from the northwest and west to the southeast and east. An outward drift into the Gulf of St. Lawrence, along the northwest coast of Prince Edward Island is inferred.

The speeds of the drift were generally greater than 3 miles a day on the average. They reached 5 miles a day (0.2 knot).

RÉSUMÉ

Plusieurs lancers de bouteilles dérivantes ont été faits dans le détroit de Northumberland, de 1960 à 1963, à de nombreux points échelonnés lors des croisières ainsi que quotidiennement à des points fixes. On a retrouvé, avant l'hiver, 1213 des 2741 bouteilles lancées. La grande moyenne du pourcentage des bouteilles retrouvées était élevée, 44%. Les nombreuses découvertes à une faible distance du lancement et la courte durée des dérives sont caractéristiques.

On peut déduire des trajets des bouteilles une dérive des eaux superficielles le long du détroit de Northumberland, du nord-ouest et de l'ouest, vers le sud-est et l'est. Un mouvement de sortie des eaux de surface du détroit dans le golfe Saint-Laurent semble aussi être une déduction logique.

Les vitesses de dérives sont habituellement plus grandes que 3 milles par jour, en moyenne. Elles peuvent atteindre 5 milles par jour (0.2 noeud).

INTRODUCTION

Northumberland Strait, lying between the Prince Edward Island and New Brunswick–Nova Scotia coasts (Fig. 1), is an important commercial fisheries area for lobster and herring. Over the past 15 years a study of abundance and distribution of lobster larvae in the northern sector has been the main biological effort (Scarratt, 1964). The program included concurrent monitoring of oceanographic conditions and drift bottle experiments during 4 years, 1960–63. Earlier circulation studies in the Strait have been reported by Dawson (1913) and Farquharson (1959, 1962).

The purpose of the present study is to show seasonal and year-to-year changes of the non-tidal drift in the northern sector of Northumberland Strait and its relation to the drift in the central and eastern sectors of the Strait,

[1]Received for publication September 17, 1964.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

as well as to that of the outside waters. The study was initiated to assist biologists interested in the circulation as it affects the biological content of the waters and the production of certain commercial species in the area. The results described here are pertinent to a very thin layer of surface waters. Work is being carried out to extend observations to a deeper layer and also along the bottom.

DRIFT BOTTLE RELEASES

Figure 1 shows the segmentation of Northumberland Strait referred to in this paper. The releases by segments were:

1. In northern Northumberland Strait (Northern and Egmont Bay segments).

   For 4 years, starting in 1960, regular releases of drift bottles were made repeatedly at one station from the end of May to October, and at two additional stations from June to September. The total number of releases every year at these stations in the northern segment varied from 116 to 206. This is called the *Pandalus* series. In June 1963, a large-scale release of 204 bottles was made at 32 positions covering both segments.

2. In central Northumberland Strait (Central segment).

   During 1961 and 1962, daily releases of drift bottles were made between Cape Tormentine, N.B., and Port Borden, P.E.I., from CNR

FIG. 1. Map of area showing the segmentation of Northumberland Strait used in this paper.

Abegweit (*Abegweit* series). From July to December 1961 and June to December 1962, 710 and 360 bottles were released, respectively.

3. In eastern Northumberland Strait (Pictou and Eastern P.E.I. segments).

   From May to December 1962, daily releases of drift bottles in the Pictou segment between Caribou, N.S., and Wood Islands, P.E.I., totalled 780 (*Selkirk* series). In June 1963, 46 bottles were released at 7 stations covering the Eastern P.E.I. segment.

4. Outside Northumberland Strait.

   During seven cruises, between 1959 and 1963, 974 bottles were released north of Northumberland Strait, along the New Brunswick coast, and at the entrance of Bay of Chaleur up to the Gaspé Peninsula in a strip 40–45 miles wide. A total of 99 and 90 bottles were released, respectively, in 1960 and 1963 between Prince Edward Island and the Magdalen Islands.

ANALYSIS OF RECOVERIES

Spatial Distribution and Inferred Drift

The overall percentage of the recoveries made in the same year as the releases was maximum for releases made in northern Northumberland Strait, at 54%. From releases made in central and eastern sectors of the Strait, recoveries were 46% and 27%, respectively. A certain number of recoveries was made after a winter season, approximating 3%, 7%, and 3% from the northern, central, and eastern sectors, respectively. Most of these bottles which were recovered in Northumberland Strait had been released in the last quarter of the year. Table I gives a summary of releases and recoveries from the fixed stations.

Table I. Summary of releases and recoveries of drift bottles from fixed stations in Northumberland Strait.

	Released	Recovered	
	No.	No.	%
Pandalus series			
1960 May–October	172	100	58
1961 May–November	206	108	52
1962 May–November	160	96	60
1963 April–October	116	51	44
Abegweit series			
1961 July–December	710	336	48
1962 June–December	360	154	43
Selkirk series			
1962 May–December	780	213	27

NORTHERN NORTHUMBERLAND STRAIT

The recoveries from the three fixed stations of the *Pandalus* series are illustrated in Fig. 2 and 3. These are seasonal recoveries totalled independently of the month of release. The distribution of recoveries by season of release would be very slightly different from that of Fig. 2 and 3, because of the short time between release and recovery.

More recoveries were made on the Prince Edward Island side than on the New Brunswick side of the Strait, indicating an easterly component of the drift of surface waters. Generally 50% or more of the recoveries — 61% on the average — are recorded in the area of release. Within the northern segment, the recoveries infer either a cyclonic eddy or a southerly drift along the New Brunswick coast and a northeasterly drift along the Prince Edward Island coast. This northeasterly movement of the surface waters is no doubt the main avenue for bottles drifting out of the northern Strait towards the Magdalen Islands, Newfoundland, Cape Breton, and the north coast of Prince Edward Island.

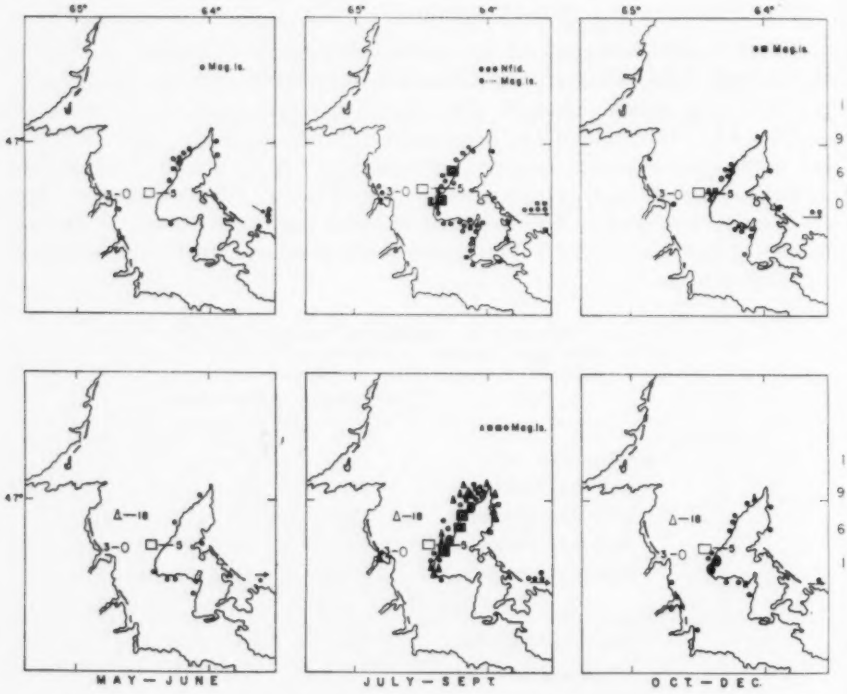


FIG. 2. Distribution of drift bottle recoveries, *Pandalus* series, from May to December 1960 and 1961. Open symbols: release stations 3, 5, and 18; closed symbols: recoveries. A small symbol represents one recovery, and a large symbol represents five recoveries.

From recoveries to the south, it is inferred that very few of the bottles that drifted into the Egmont Bay segment drifted further into the Bedeque Bay segment. The circulation in the Egmont Bay segment seems to be that of an eddy with inflow from the north along the New Brunswick coast and main outflow to the north along the Prince Edward Island coast. A predominant easterly drift is inferred from the large number of recoveries along the Prince Edward Island coast.

Even though the releases at fixed stations are few, the rates of recovery, 40–70%, are sufficient to show seasonal and year-to-year variations. The relative number of recoveries on the New Brunswick side of Northumberland Strait has a tendency to increase from summer to autumn. As shown in Table II, the percentage recovery from fixed station releases has a tendency to be minimum for July and maximum for September. The low percentage in July seems to be associated with a small proportion of recoveries within the area of releases, the northern segment, and a large proportion of recoveries away from it, either outside the Strait or in the Egmont Bay and Bedeque segments. However, a seasonal high percentage recovery is not necessarily associated

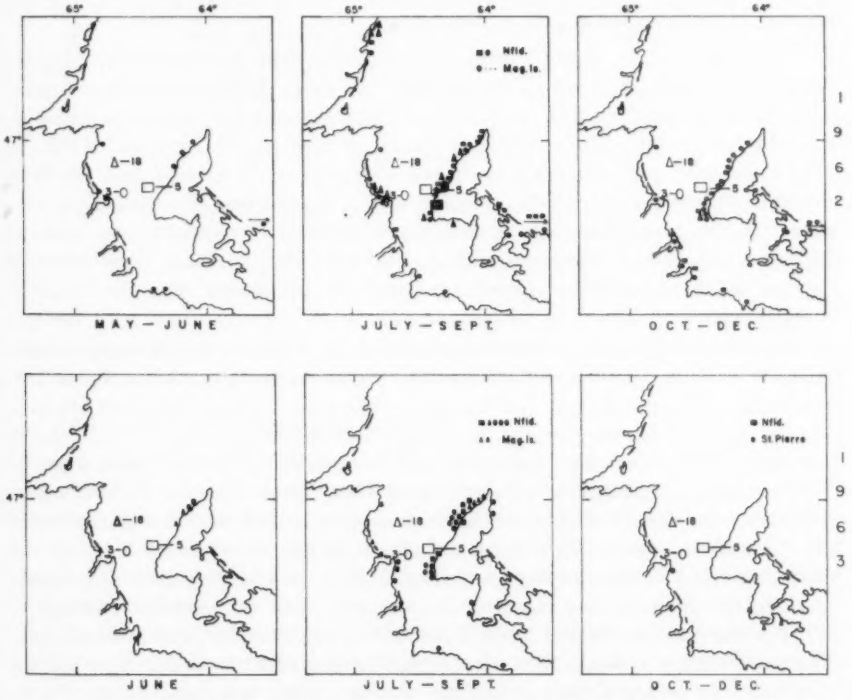


FIG. 3. Distribution of drift bottle recoveries, *Pandalus* series, from May to December 1962 and 1963. Open symbols: release stations 3, 5, and 18; closed symbols: recoveries. A small symbol represents one recovery, and a large symbol represents five recoveries.

TABLE II. Drift bottle recoveries from releases made during July and September in the northern segment, 1960–64.

	July	September
Number of releases:	128	86
Recoveries:		
in northern segment (area of release)	20	33
in Egmont Bay and Bedeque segments	13	18
outside Northumberland Strait	18	10
Total number	51	61
Percentage recoveries	40	71

with a large proportion of recoveries within the area of release. The conditions which seem to be prevalent in July are those of either divergence or dispersion from the area or rapid flushing of the area.

As shown in Fig. 2 and 3, during 1961 and 1963, a relatively high proportion of recoveries occurred in the northern segment, the area of release, associated with a relatively low proportion in the Egmont Bay segment and outside the Strait. Opposite conditions were predominant in 1960 and 1962. In 1963 the overall percentage recovery was the smallest in 4 years, and the July conditions described earlier still existed. Other contrasting conditions are also shown in the Magdalen Islands and Newfoundland recoveries; they amount to 16% of all the outside recoveries in 1962 and 80% in 1963. This could be an indication of stronger circulation over the Magdalen Shallows in 1963 than in 1962.

The recoveries from the releases made during June 1963 at several stations covering both northern and Egmont Bay segments are grouped in Table III. They infer a circulation pattern similar to that deduced from the fixed stations releases and recoveries; namely, a strong movement from west to east in the northern and Egmont Bay segments, and as an eddy in the northern segment confirming a northeasterly current along the Prince Edward Island coast. However, the inferred drift of surface waters towards the central segment of the Strait, and even east of it, is more definite than previously observed. For the bottles released in the northern segment, 31% of all the recoveries were made south of the Egmont Bay segment, as compared with the previous average of 2%. For the bottles released in the Egmont Bay segment, 86% followed a southeasterly direction towards the central and eastern sectors of the Strait. As a corollary, the inferred drift of surface waters to the east past North Point, P.E.I., was rather restricted, since only 10% of all the recoveries were recorded outside the Strait. The conditions in the second half of June 1963 were those

TABLE III. Drift bottle recoveries from releases made in June 1963 in northern and Egmont Bay segments.

	Northern segment	Egmont Bay segment
Number of releases	156	48
Number of recoveries in:		
Northern segment		
P.E.I. side	37	–
Mainland	–	–
Egmont Bay segment		
P.E.I. side	20	3
Mainland	3	1
Bedeque Bay segment		
P.E.I. side	3	–
Mainland	12	5
Central segment		
P.E.I. side	5	7
Mainland	8	5
Pictou and eastern P.E.I. segments		
P.E.I. side	4	2
Mainland	1	5
Outside	12	1

of relatively strong circulation through Northumberland Strait. This had not been observed before. It is not surprising that such differences should occur between recoveries from cruise-type releases involving a large number within a short time, and recoveries from fixed station-type releases involving repeated releases of a small number of bottles at regular intervals. The former gives inferences of the circulation over a short period of time, the latter of the average circulation over a wide range of conditions.

CENTRAL NORTHUMBERLAND STRAIT

A large number of drift bottles was released in the central part of Northumberland Strait between Cape Tormentine, N.B., and Port Borden, P.E.I. This was termed the *Abegweit* series. For the summer releases, 1961 and 1962, the percentage recovery (67%) was greater, on the average, than for the *Pandalus* series (52%). The percentage recovery decreased for those released during the autumn.

The seasonal recoveries in 1961 and 1962 are shown in Fig. 4 and 5, respectively. The salient features of the recoveries are: (1) their large proportions on the Prince Edward Island side in comparison with the New Brunswick side; (2) their concentrations at a short distance from the point of release; (3) their relative spread to the east and their absence in the Egmont Bay

segment. The inferred predominant drift from the mainland to Prince Edward Island was relatively stronger in 1961 than in 1962. This west–east drift seems to weaken during the autumn (October–December) as compared with the summer (July–September). The same variations were inferred from recoveries of the *Pandalus* series.

The *Abegweit* series, similar to the *Pandalus* series, inferred a somewhat restricted drift. However, there is an inference of a definite southeasterly drift from the central segment into the Pictou segment but only occasionally further to the east. The much less frequent westerly drift towards the Bedeque Bay segment seems to increase from summer to autumn.

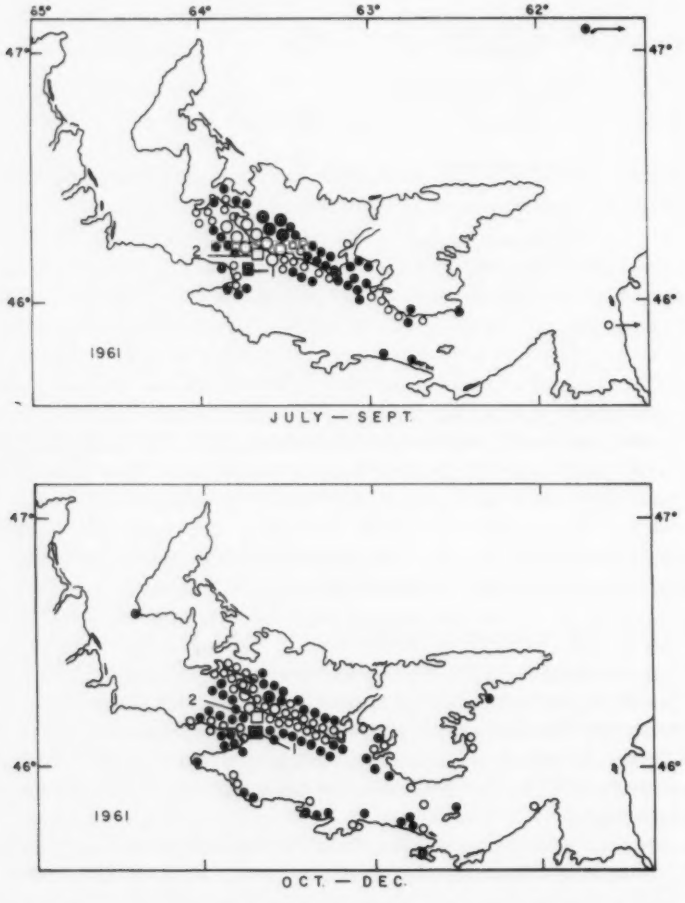


FIG. 4. Distribution of drift bottle recoveries, *Abegweit* series, from July to December 1961. Squares: release stations 1 and 2; circles: recoveries. A small circle represents one recovery, and a large circle represents ten recoveries.

EASTERN NORTHUMBERLAND STRAIT

In 1962 only, the eastern sector of Northumberland Strait was studied at the same time as the central and northern sectors. The overall percentage recovery from the *Selkirk* series released between Wood Islands, P.E.I., and Caribou, N.S., was 27%, the lowest of the three series in Northumberland Strait. It was 35% for summer month releases, still the lowest of the three series.

As inferred from the recoveries (Fig. 6), a predominant drift from the mainland to Prince Edward Island is one of the features of spring and summer seasons. There is almost a reverse of this drift during autumn. There is also

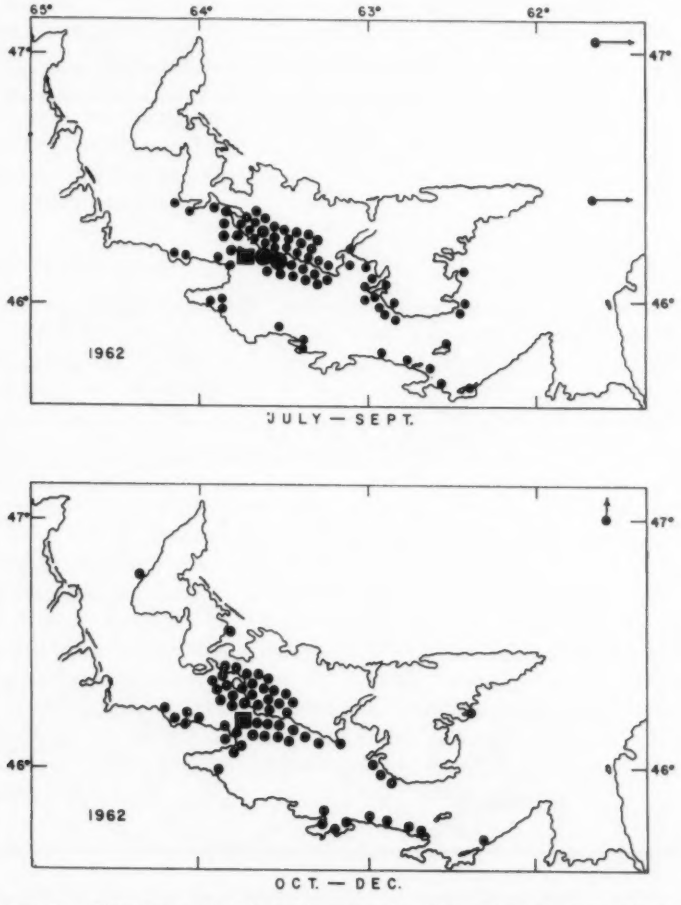


FIG. 5. Distribution of drift bottle recoveries, *Abegweit* series, from July to December 1962. Squares: release station; circles: recoveries. A small circle represents one recovery, and a large circle represents ten recoveries.

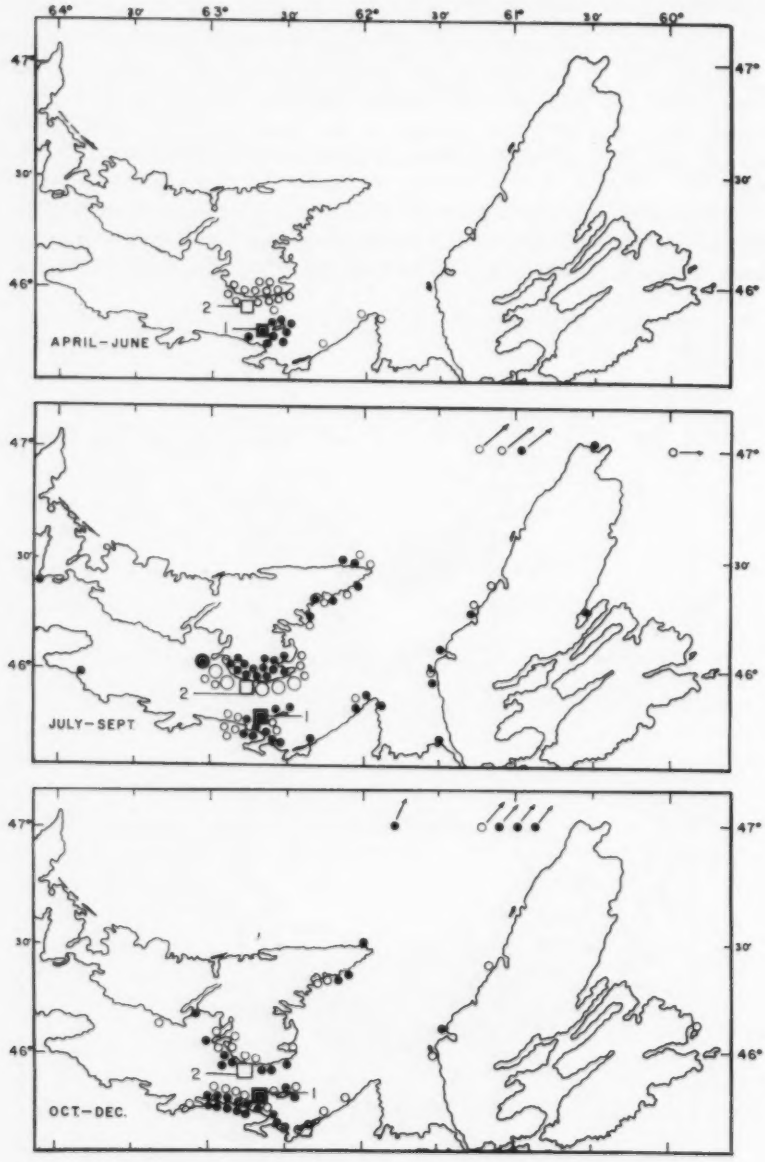


FIG. 6. Distribution of drift bottle recoveries, *Selkirk* series, from April to December 1962. Squares: release stations 1 and 2; circles: recoveries. A small circle represents one recovery, and a large circle represents ten recoveries.

a certain amount of westward drift but it hardly extends into the central segment. A definite easterly drift from the Pictou segment to the eastern P.E.I. segment and beyond is inferred. From the summer releases, 22% of all the recoveries are recorded to the east more than 20 miles from the point of release, and 15% more than 40 miles away. At the same time 75% of all recoveries were observed within 15 miles of the point of release. There is no strong evidence of drift on the south side of the Strait opposite to that on the north side.

In June 1963, 46 drift bottles were released at seven stations in the eastern P.E.I. segment at approximately the same time other releases were conducted in the northern end of the Strait. A percentage recovery of 50% was recorded for the releases in the eastern P.E.I. segment. More than half of these recoveries infer an easterly drift towards outside the area of release, while the others infer a westerly drift, up to 25 miles west of the point of release. There are similarities between the northern segment and the eastern P.E.I. segment. To someone in Northumberland Strait, looking towards the open Gulf, there seems to be a southward drift on the left hand side of the segments and a northeasterly drift on the right hand side. The presence of cyclonic eddies is inferred in both cases.

OUTSIDE RELEASES

On several occasions, drift bottles were released during cruises in the vicinity of Northumberland Strait. The surface non-tidal drift over the southwestern Gulf of St. Lawrence as inferred from drift bottle recoveries seems to be generally to the south and to the east (Bumpus and Lauzier, 1964). It is important to assess the contribution of outside waters to Northumberland Strait. From 974 bottles released north of the Strait, 247 bottles were recovered (before winter) in various parts of the Gulf. Less than 9% (21) of all recoveries or 2.2% of all releases were reported from Northumberland Strait, most of them in the northern segment, and none as far as the central segment. These originated only from some of the cruises.

The inferred circulation in the area north of Northumberland Strait seems to be in most cases to the southeast or east and in at least 10% of the cases to the south towards the Strait. However, it is impossible to estimate the extent of a southerly drift which makes a "u-turn" in northern Northumberland Strait: into the northern segment along the New Brunswick coast and out into the Gulf again along the Prince Edward Island coast. It seems that Northumberland Strait does receive on the average a rather small "share" of the surface waters just north of it.

Time Distribution and Inferred Speed

The overall percentage recoveries for the summer month releases in 1962 were 63%, 61%, and 35% for the *Pandalus*, *Abegweit*, and *Selkirk* series, respectively. The time taken to recover a definite proportion of released bottles

varies from one series to the other, depending on their location in the Strait. From the *Abegweit* series, 25% of the releases in the central segment were recovered within 10 days; from the *Pandalus* series, 25% of the releases in the northern segment were recovered in 17 days; and from the releases in Pictou segment, the *Selkirk* series, 25% were recovered in 23 days.

Such a short lifetime afloat of an *Abegweit* bottle is not surprising if one considers the geographical location of the points of release, the predominant drift from the mainland to Prince Edward Island, and the rate of recovery within 10 miles of the point of release — 67% of all recoveries. It took a longer time to recover 25% of the bottles from *Pandalus* and *Selkirk* series because these were released in wider parts of the Strait which are adjacent to the open Gulf. The time given for "25% recovery" is not constant for a given segment but the shorter period always seems to be characteristic of the *Abegweit* series, released in the central segment.

The inferred speed of surface drift has been calculated in two different ways, after eliminating the recoveries recorded within 10 miles from the point of release. First, an average speed was computed from the fastest bottles (the upper third of the speed frequency) irrespective of the distance travelled outside the 10-mile radius; this was the technique used by Bumpus and Lauzier (1964). Second, another average speed was computed from most of the bottles which had travelled a certain distance, always greater than 10 miles; some very slow ones were excluded.

In using the fastest bottles an attempt was made to show seasonal variations of speed and direction; however, no such attempt was made with the other technique. The average speeds are listed in Table IV. As expected, the speeds computed for trips longer than 20 miles are approaching the values calculated for the fastest bottles. In general, the longer the "trip", the faster

TABLE IV. Average surface drift in miles per day from June to October.

Series segment	*Pandalus* northern	*Abegweit* central	*Selkirk* Pictou
Fastest bottles[a]	4.5 (NE)	3.5	3.5
	3 (SE)		
Most bottles			
10–15-mile trips	1.6	1.3	1.8
15–20-mile trips	2.9	1.3	1.5
20–50-mile trips	3.7	3.3	2.3
>50-mile trips	3.5	–	2.7

[a]Upper third of the speed frequency and drifts of 10 miles or more.

is the drift. Possibly a short trip may be a series of drifts back and forth or drifts around an eddy and ending not too far from the point of release. A longer trip may be a more straightforward drift free from aleatory motion. It should be realized that the speed values listed here are minima and in some cases may be much smaller than the actual speed of the drift. However, they represent the speed of a thin surface layer 18–20 cm deep. The residual currents recorded by the Canadian Hydrographic Service (Farquharson, 1959) are of somewhat lower strength. They vary generally between 1 and 2 miles a day and represent the speed of a residual current at a depth of 7 m.

In the northern segment, the northeast drift always seemed to be faster than the southwest drift by a factor that varies between 1.3 and 2.5. The maximum speeds occurred in July for the northern segment and from June to August for the Pictou segment. They may reach 5 miles a day. There were no seasonal tendencies in the inferred speeds for the central segment.

DISCUSSION

Because of the high proportion of local recoveries, the three series *Pandalus*, *Abegweit*, and *Selkirk* seem to indicate that they are three "stocks" that do not "intermingle". Most recoveries infer a drift to a certain point along the Strait but very seldom further. There seems to be a drift from northwest to southeast at various points along the Strait. Bottles released in a relatively small body of water have a short average lifetime and are subjected to a high rate of recovery. From the rate of recovery, the average speed, and the distance to be travelled to go from one area of release to the other, it is possible to estimate the chances for bottles released in the central segment of the Strait to drift into another area of release. With an average speed of 2 miles a day, it would take 25 days to reach another area of release; by that time, 40–45% of the bottles released would have already been recovered. In the case of the bottles released in the northern segment, the assumed speed is higher and the rate of recovery within the first month, lower. Then 25% of the bottles released would have been recovered before being able to reach the area of release in the central segment, if all the bottles had drifted into the segments to the southeast. In fact only 15% did so. Consequently the experiment cannot demonstrate continuity of flow.

The recovery charts (Fig. 2–6) do not imply a continuous drift from one end of the Strait to the other. However, the similarities in the speeds within various segments, the consistency and some predominance of southeasterly and easterly drift, as well as the lack of long drifts westward in the central and Pictou segments infer a resultant drift of surface water in Northumberland Strait from the northwest to the southeast. Figure 7 shows the average surface circulation in Northumberland Strait as inferred from drift bottle releases and recoveries. The inference of a resultant drift from the northwest to the southeast is strengthened by consideration of the seasonal variations of salinity conditions. During the summer, a large body of relatively low salinity

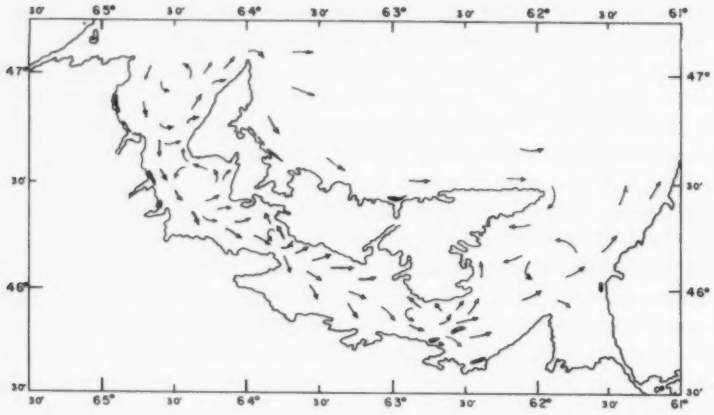


FIG. 7. The inferred non-tidal drift in Northumberland Strait.

water drifts southward over the Magdalen Shallows. A summer minimum of salinity is also observed in Northumberland Strait (Lauzier, 1957).

It was mentioned previously that, in general, the relative distribution of recoveries from the July *Pandalus* series is different from average conditions. It was presumed then that either dispersion or rapid flushing occurred in the area. Approximately at the time there is a summer minimum of salinity and a definite gradient of salinity between the western and eastern ends of Northumberland Strait which might be partly responsible for a stronger circulation through the Strait, or at least in both the northern and Egmont Bay segments.

The predominant drift in Northumberland Strait from the mainland to Prince Edward Island during the summer months was observed to diminish during the autumn all over the Strait and almost to the point of a reversal in the Pictou segment. This might be associated with the weakening of the southwest winds and the strengthening of the easterly winds in the autumn. Although the outside contributions to Northumberland Strait from the north are generally small, they were greater in June and August 1959 and May 1960 than at any other time of observation. From one cruise as many as 23% of the recoveries were reported in Northumberland Strait. In most cases, when bottles were recovered in the Strait, the resultant winds (as observed at Summerside, P.E.I.) had either a stronger easterly or a weaker southerly component than usual. When bottles released outside were not recovered in the Strait, the resultant winds seemed to have a stronger component than usual from either the south or the west. These are the only relationships found so far, between the direction of the surface drift and the resultant winds on a monthly basis.

It is assumed that the bottles drift with the water and its biological content such as lobster and herring larvae. Drift bottle observations give some of

the history of particles of water (Lagrangian observations) in contrast with current-meter observations which give the history of what goes on at one point (Eulerian observations) without knowledge of origin or past history of the particles in motion. Most biological and oceanographic observations are of the Eulerian type. The circulation of the surface waters in Northumberland Strait illustrated in Fig. 7 should be taken as the most probable circulation pattern under various conditions. From the data on hand it is impossible to say how constant and how fast is the renewal of waters and the biological content in a given segment, or how long the water stays in a segment. However, eddies seem to exist at both ends of the Strait. There is a northwest–southeast drift through the Strait but it is not known if this inferred drift is counterbalanced by a reverse drift which is impossible to observe because of the prevalent onshore drift along Prince Edward Island. It is hoped that the answers to this and many other unknowns concerning water circulation in Northumberland Strait will be revealed through further research.

SUMMARY

The surface circulation in Northumberland Strait has been studied from drift bottle experiments at fixed stations and during cruises. Emphasis was given to the northern sector of the Strait, starting in 1960, but the studies covered the whole Strait in 1962. From releases of 2741 bottles in 1960 to 1963 the overall percentage recovery was 44%. The percentage recovery for a year or for the summer months was generally higher (above 60%) in the northern part of the Strait, and lower (less than 40%) in the eastern end of the Strait.

The main features of the inferred surface non-tidal drift are:

1. A general movement of the surface waters through the Strait from the northwest and west to the southeast and east.
2. A predominant drift from the mainland to Prince Edward Island, stronger in the summer than in the autumn.
3. A cyclonic eddy in the northern entrance of the Strait with a southerly drift along the New Brunswick coast and northeasterly drift along the Prince Edward Island coast, the latter being the main avenue towards the open Gulf.
4. Other eddies are suggested mainly south of West Point, P.E.I., and at the eastern entrance of the Strait.
5. The speeds seem to vary seasonally in certain parts of the Strait. They are generally greater than 3 miles a day on the average, and may reach 5 miles a day.

In general the rate of drift bottle recoveries is high for the releases made in the central part of the Strait, where 25% of the bottles released are recovered within 10 days. It takes 17 and 23 days to recover the same proportion of those released in the northern and southern ends, respectively.

ACKNOWLEDGMENTS

The author is indebted to Dr D.G. Wilder of the lobster investigations at the Biological Station, St. Andrews, N.B., for his assistance in organizing the drift bottle releases from M.V. *Pandalus II* starting in 1960; to the masters of *Pandalus II* (Fisheries Research Board), of *Abegweit* (Canadian National Railways), and of *Lord Selkirk* (Northumberland Ferries) for their co-operation in the task of drift bottle releases. The assistance of Messrs J.G. Clark and A.W. Brown in the organization and co-ordination of releases and in the compilation of drift bottle data is gratefully acknowledged. Drift bottle data related to outside releases in 1959 were supplied to the author by Dr Y.M.L. Jean.

REFERENCES

BUMPUS, D. F., AND L. M. LAUZIER. 1964. Surface circulation on the continental shelf off eastern North America between Newfoundland and Florida. Folio 7. Serial Atlas of the Marine Environment, American Geographical Society, New York.

DAWSON, W. B. 1913. The currents in the Gulf of St. Lawrence. Dept. of the Naval Service, Ottawa.

FARQUHARSON, W. I. 1959. Causeway Investigation Northumberland Strait. Report on Tidal Survey 1958. Dept. Mines and Technical Surveys, Ottawa, 137 pp.

1962. Tides, tidal streams and currents in the Gulf of St. Lawrence. Dept. Mines and Technical Surveys, Ottawa, 76 pp.

LAUZIER, L. M. 1957. Variations of temperature and salinity in shallow waters of the southwestern Gulf of St. Lawrence. *Bull. Fish. Res. Bd. Canada*, No. 111, pp. 251–268.

SCARRATT, D. J. 1964. Abundance and distribution of lobster larvae (*Homarus americanus*) in Northumberland Strait. *J. Fish. Res. Bd. Canada*, **21**(4): 661–680.

Effect of Photoperiods on the Behavior of Juvenile Atlantic Salmon (*Salmo salar* L.) in Vertical and Horizontal Light Gradients[1, 2, 3]

By A. T. Pinhorn[4] and C. W. Andrews

Memorial University of Newfoundland
St. John's, Nfld.

ABSTRACT

The behavior of juvenile Atlantic salmon in vertical and horizontal light gradients was studied. Comparisons were made between the behavior of fish exposed to 16-hr photoperiods (long-photoperiod fish) and fish that had not been so conditioned (control fish). In vertical light gradients the long-photoperiod fish were very active and moved rapidly up and down the water-column. At low light intensities they tended to rise into the surface layers. Peak activity and the greatest numbers in the upper reaches of the water-column occurred at 0.04 ft-c (lowest intensity studied). The control fish, however, were relatively quiescent at all light intensities and settled to the bottom at low light intensities. Peak activity and the greatest numbers in the upper reaches of the water-column occurred at 1.0 ft-c. In horizontal light gradients the control and long-photoperiod fish remained in areas of lowest light intensities. When allowed to remain in the light gradients for a short period of time, both groups showed a stronger avoidance of light sources of higher intensity but moved into the brighter areas with low intensity light sources. With prolonged stay in the light gradients, these trends were essentially reversed due to nipping and defence of territory. The long-photoperiod fish showed a stronger avoidance reaction than the control fish with the 100-watt light source, whereas the reactions of both groups were similar with the 7½-watt and 300-watt light sources, when these fish were allowed to remain in the gradients for a short period of time. However, with prolonged stay in the gradients, nipping and defence of territory resulted in a stronger avoidance reaction by long-photoperiod fish to all light gradients. The differences in the behavior of control and long-photoperiod fish in vertical and horizontal light gradients is believed to be a result of exposure of the latter to controlled photoperiods.

INTRODUCTION

A review of the literature on the effect of exposure to light on the maturity and spawning of fish was presented in Pinhorn and Andrews (1963). In the same paper a review of the pertinent literature on the physical, biochemical, and behavioral changes at the time of parr–smolt transformation of Atlantic and Pacific (*Oncorhynchus*) salmon revealed that the behavior patterns of the parr are distinctly different from those of the smolts. In view of this it was postulated that exposure of juvenile Atlantic salmon to controlled photoperiods might have an effect on the timing of the parr–smolt transformation which

[1]Received for publication August 5, 1964.
[2]This paper is based on a section of a thesis submitted by the senior author in partial fulfilment of the requirements for the degree of Master of Science in Zoology at the Memorial University of Newfoundland.
[3]This investigation was supported by a grant from the National Research Council of Canada to Dr C. W. Andrews.
[4]Present address: Fisheries Research Board of Canada Biological Station, St. John's, Nfld.

J. Fish. Res. Bd. Canada, 22(2), 1965.
Printed in Canada.

might result in differences in the behavior patterns of fish exposed to photoperiods and those exposed to control conditions. This was used as a working hypothesis. The present paper uses the same hypothesis and compares the differences in the behavior of the two groups of fish in vertical and horizontal light gradients.

MATERIALS AND METHODS

The source of the juvenile Atlantic salmon used in these experiments and the procedure of feeding are identical to those described in Pinhorn and Andrews (1963). The long-photoperiod fish were subjected to light of 25 ft-c intensity for 16 hr each day and darkness for the remaining 8 hr. The control fish were subjected to light of less than 1 ft-c intensity for 16 hr each day and darkness for the remaining 8 hr. The conditions of temperature to which the fish were subjected in the holding tanks are given at the beginning of the appropriate section together with the details of the exposure times of long-photoperiod fish.

The vertical light gradient experiments were conducted during August 1959 and the fish used were 17 months old. The horizontal light gradient experiments, Series I, were conducted during July and August 1959 and the fish used were 16 months old. The horizontal light gradient experiments, Series II, were conducted during October and November 1959 and the fish used were 20 months old. They ranged in length from approximately 2 to 4 cm at the beginning of the study to 6–8 cm at the end.

Chi-square tests and *t*-tests were used in analysing the results. However, their use can probably be questioned on the basis that the observations are never independent. Each position which a fish occupies will bias its next position. Nevertheless, it is felt that the tests are useful in that they indicate trends in behavior.

Vertical Light Gradients

The apparatus used in the study of behavior in vertical light gradients consisted of a cylindrical tank, 86 cm high and 56 cm in diameter, painted gray on the inside (Fig. 1). A cylindrical-shaped shield consisting of wire netting surrounded by black cloth was placed over the top of the tank and fitted neatly around the top rim on the tank. At the top of the shield a cardboard cover was placed and the fish were observed from above through a peephole in the cover. The particular light in use was also suspended through this cover, giving a vertical light gradient decreasing from the top of the tank to the bottom. The particular light intensity in use refers to the light intensity at the surface of the water. Incandescent lamps of $7\frac{1}{2}$ w, 25 w, and 40 w were used to obtain the desired intensities.

At the beginning of an experiment 10 fish were placed in the tank, the light was turned on, and the fish were left undisturbed for 30 min. At the end of this time the number of fish in the upper one-third of the tank was counted

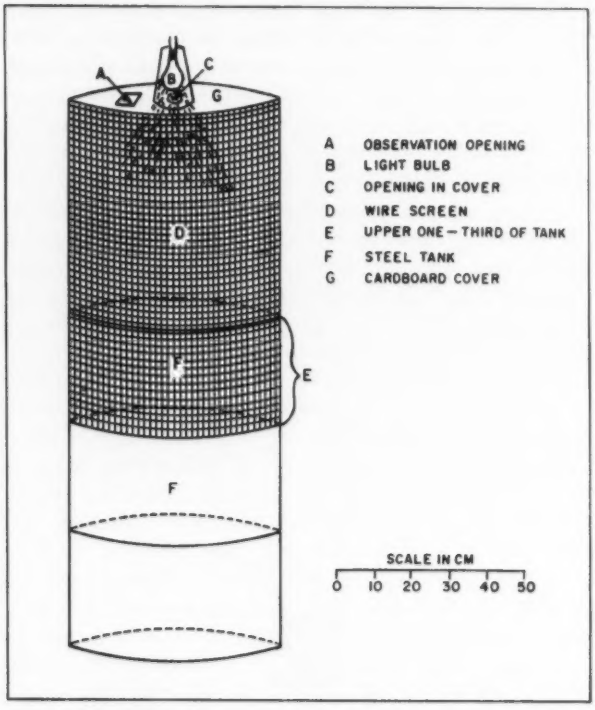


FIG. 1. Diagram of apparatus used in the study of the behavior of juvenile Atlantic salmon in vertical light gradients.

at 1-min intervals for a period of 10 min, giving a total of 10 counts. A different group of 10 fish was then placed in the tank and the experiment was repeated with a procedure identical to the first. Five of these experiments were performed at light intensities of 0, 0.04, 0.2, 1.0, and 5.0 ft-c for both control and long-photoperiod fish, giving a total of 50 counts or 500 positions plotted at each light intensity. Observations at 0 ft-c (darkness) were made by momentarily flashing on a light of 0.04 ft-c intensity; the fish were not disturbed in this operation. When plotting the percentage values of fish in the upper one-third portion of the tank in Fig. 3, the values at 0 ft-c were plotted at 0.008 ft-c the next lowest ratio to 0.04 ft-c, because of the impossibility of plotting a 0 value on a logarithmic scale.

HORIZONTAL LIGHT GRADIENTS

The experiments designed to study the behavior of fish in horizontal light gradients were divided into two groups, referred to as Series I and Series II. The apparatus for both groups of experiments consisted of a rectangular tank 244 cm long, 30 cm wide, and 28 cm deep, painted gray on the inside (Fig. 2).

At 30-cm intervals along the tank black lines were painted transversely dividing it into seven compartments. These were numbered I–VII. A screen was placed at the end of compartment VII so that the fish would be confined to the area occupied by compartments I–VII and would be prevented from entering the 34-cm end area containing an overflow pipe. The opposite end of the tank was glass to which a light and light reflector were attached. This gave a horizontal light gradient decreasing from high intensity at the glass end to low intensity at the other end. Three different incandescent lamps were used, 7½-w, 100-w, and 300-w, giving three light gradients. Unfortunately the illumination in each compartment was not measured.

In the Series I experiments the fish were observed from behind a black curtain hung along one side of the tank. Because the room was in darkness,

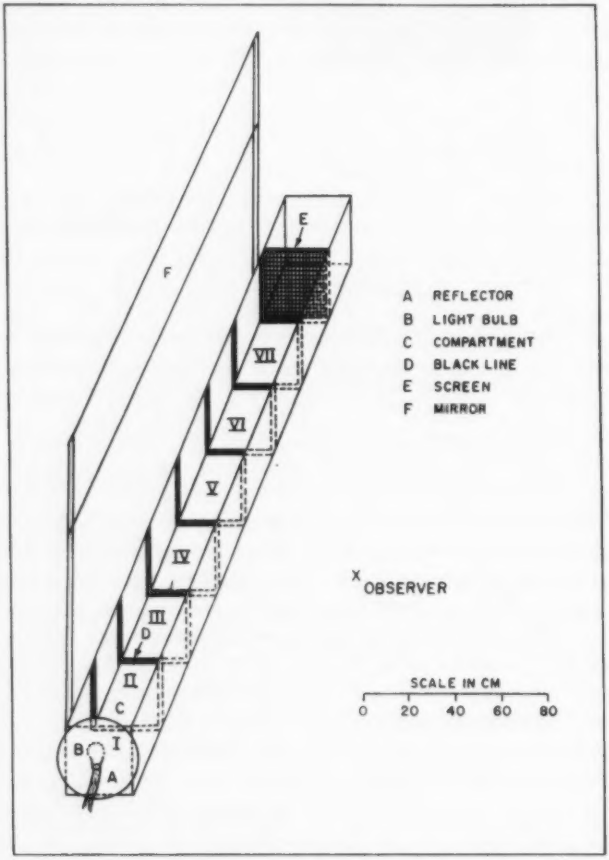


FIG. 2. Diagram of apparatus used in the study of the behavior of juvenile Atlantic salmon in horizontal light gradients.

except for the light at the end of the tank, apparently the fish were not disturbed during observation. In the Series II experiments a mirror was mounted above the tank so that the fish were observed from below the tank. During a Series I experiment no water flowed into the tank but the temperature remained fairly constant and within 1.0°C of the acclimation temperature. A slight flow of water was allowed to run into the tank in the Series II experiments to prevent the temperature from rising during the experimental period, but this was not strong enough to elicit a rheotactic response.

In the Series I experiments the trough was filled with water at the desired temperature, 10 fish were placed in the tank, and the light was turned on at the end of the tank. The fish were then allowed 30 min to take position in the light gradient. The number in each compartment was then counted at 1-min intervals for a period of 10 min, giving a total of 10 counts per experiment. Five experiments were performed using five different groups of fish with each lamp used, giving a total of 50 counts per lamp.

In the Series II experiments the trough was filled with water at the desired temperature, 14 fish were placed in the tank in the evening and the apparatus was left overnight with the light on at the end of the tank and the remainder of the room in darkness. Observations began at 9 AM the following morning. The positions of the fish with respect to compartments I–VII were recorded at 30-sec intervals for a period of 20 min, giving a total of 40 counts (560 positions). This was repeated at noon, 3 PM, and 6 PM. The fish were then left overnight and the observations were repeated the following day. In all, a total of 280 or 320 counts (3920 or 4480 positions) were obtained in each experiment, depending on whether there were seven or eight observation periods. The fish were then removed from the tank and a different group of 14 fish was used. The experiment was then repeated with a procedure identical to that above; this was considered a duplicate experiment. Therefore, if the duplicate experiments are combined, a total of 560 or 640 counts (7840 or 8960 positions) was obtained.

No attempt was made to distribute the fish randomly in the horizontal light gradient tank, when transferring them from the holding tanks, in either the Series I or the Series II experiments. However, this had little effect on the eventual location of the fish since they swam rapidly to and fro in the tank for the first few minutes after transfer.

RESULTS

General Observations

VERTICAL LIGHT GRADIENTS. During this study, control and long-photoperiod fish exhibited marked differences in behavior. As a rule, control fish showed very little activity at any of the light intensities studied. When placed in the experimental tank they remained on the bottom for the first 5–10 min, after which some of them began to swim slowly up the sides of the tank. The maximum number in the upper one-third of the tank was six fish on one occasion, with the average being one to two fish. The movements of these control

fish were very slow and it took a fish approximately 1 min to traverse the 85 cm column of water. On many occasions the fish were seen to remain motionless for minutes at a time, with only slow undulations of the tail and fins serving to offset the opercular breathing movements. More activity was noted at higher than at lower light intensities.

The long-photoperiod fish showed a marked difference in the amount of activity manifested. At all light intensities these fish exhibited some surfacing behavior, the absolute amount varying inversely with the light intensity at the surface of the water. The concentration of fish seemed to move up and down the column of water as the light intensity was increased or decreased. Sometimes, at low light intensities, one or more fish would swim into the upper layer of water with the dorsal fin protruding and the nose being pushed at intervals above the surface of the water. If startled the fish would dart to the bottom of the tank but would return to the surface shortly thereafter. At the light intensity of maximum activity described below, these fish were so active that they would swim up and down the water column with the result that a greater percentage remained in the upper one-third portion of the tank than with any other light intensity. This vertical wandering resulted in considerable position variation for the long-photoperiod fish.

From qualitative observations it seems that these salmon show positive thigmotaxis, because they usually followed the walls of the tank very closely when rising to the surface of the water. Nipping and defence of territory were also frequently observed in these experiments.

HORIZONTAL LIGHT GRADIENTS. Both control and long-photoperiod fish showed similar general behavior in the horizontal light gradients. When first placed in the tank, with the light on at one end, the fish swam from one end to the other. Schooling was not studied in detail but, qualitatively, the long-photoperiod fish seemed to show a closer aggregation than the control fish in this to-and-fro movement. Within an hour after transfer to the tank, the fish had become quiescent and had taken position in the different compartments. Some of these compartments were later defended by groups of fish and individuals. Nipping and defence of territory were not studied in detail but general observations indicated that this behavior occurred more frequently in the Series II than in the Series I experiments and more frequently among control fish than long-photoperiod fish.

BEHAVIOR OF FISH IN VERTICAL LIGHT GRADIENTS

The fish used in the vertical light gradient experiments were acclimatized to water of 15°C. The long-photoperiod fish had been subjected to a total of 1376 hr (86 days) of light and 688 hr (86 days) of darkness when the experiments began and 1536 hr (96 days) of light and 768 hr (96 days) of darkness when the experiments ended. For comparison, the total hours of daylight from sunrise to sunset for the same period amounted to 1331 hr at the beginning of the experiments and 1468 hr at the end of the experiments.

CONTROL FISH. The variations in the numbers of control fish in the upper one-third portion of the experimental tank were fairly large in some cases (Fig. 3).

At all light intensities the percentages of fish in the upper one-third portion of the tank were significantly less than the expected value of $33\frac{1}{3}\%$ if random distribution existed (Fig. 3). In fact P-values corresponding to chi-square values based on total numbers of fish in the upper one-third portion were all less than 0.001. This indicates that the control fish were reacting negatively to the light in this vertical gradient and were remaining in the lower two-third section of the tank. Peak activity for these fish occurred at 1.0 ft-c where the proportion of fish in the upper one-third was significantly greater than that at 0, 0.04, and 0.2 ft-c below it or 5.0 ft-c above it (Fig. 3). P-values corresponding to *t*-values based on differences in the proportions of fish in the upper one-

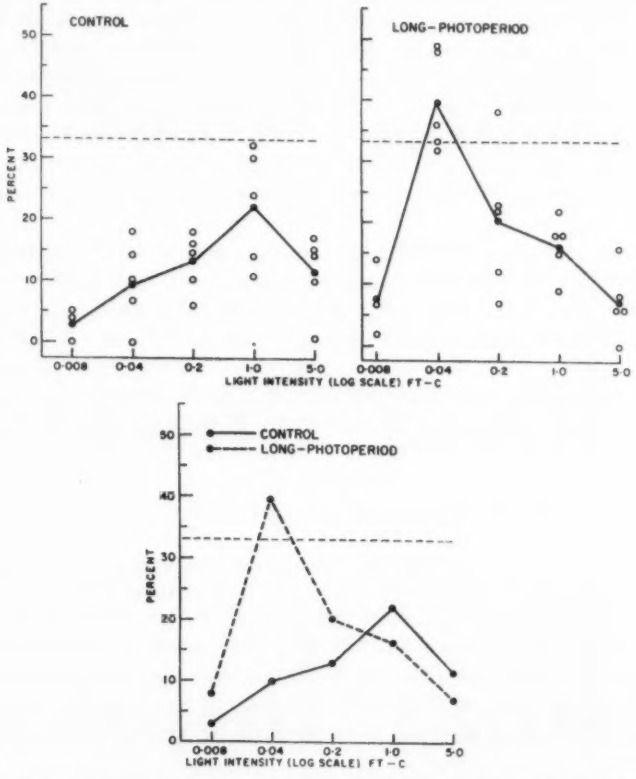


FIG. 3. Percentages of juvenile Atlantic salmon in the upper one-third portion of the vertical light gradient tank at different light intensities. The broken horizontal line represents the percentage expected if random distribution existed. Open circles are averages of individual experiments. Closed circles are averages of all experiments.

third at different light intensities were all less than 0.001. At 0 ft-c (darkness) only an average of 3% was found in the upper one-third of the tank. These results indicate that control fish showed no significant surfacing reaction (movement into the surface layers) even at their maximum activity (1.0 ft-c) and at low light intensities and in darkness they tended to settle to the bottom and become very inactive.

LONG-PHOTOPERIOD FISH. The variations in the numbers of long-photoperiod fish in the upper one-third of the tank were of the same order as those for the control fish (Fig. 3).

At 0, 0.2, 1.0, and 5.0 ft-c the percentages of fish in the upper one-third of the tank were significantly less than the expected value of $33\frac{1}{3}\%$ if random distribution existed (Fig. 3). Chi-square tests yielded P-values of less than 0.001 in each case. However, at 0.04 ft-c the proportion of fish in the upper one-third portion was significantly greater than the expected value ($P = 0.004$) (Fig. 3). Maximum activity for these fish occurred at 0.04 ft-c where *t*-test showed that the proportion in the upper one-third was significantly greater than at 0 or 0.2 ft-c ($P < 0.001$ in each case) (Fig. 3). There was no significant difference between the reactions at 0.2 and 1.0 ft-c ($P = 0.50$) but a significant decrease in activity did occur at 5.0 ft-c where the proportion was significantly less than at 1.0 ft-c ($P < 0.001$) (Fig. 3). All of these comparisons indicate that the long-photoperiod fish showed a definite surfacing reaction at the lowest intensity.

COMPARISON OF CONTROL AND LONG-PHOTOPERIOD FISH. There was a significantly greater proportion of long-photoperiod fish in the upper one-third of the tank at 0, 0.04, and 0.20 ft-c whereas there was a significantly greater proportion of control fish in this portion at 1.0 and 5.0 ft-c ($P < 0.05$ in each case) (Fig. 3). Thus, at low light intensities the long-photoperiod fish were very active and rose into the surface layers, whereas the control fish were inactive and sank to the bottom. The reverse was true at higher light intensities.

BEHAVIOR OF FISH IN HORIZONTAL LIGHT GRADIENTS

The fish used in the horizontal light gradient experiments, Series I, were acclimatized to water of 15°C. The long-photoperiod fish had been subjected to a total of 4480 hr (280 days) of light and 2240 hr (280 days) of darkness when the experiments began and 4704 hr (294 days) of light and 2352 hr (294 days) of darkness when the experiments ended. For comparison, the total hours of daylight from sunrise to sunset for the same period amounted to 3309 hr at the beginning of the experiments and 3522 hr at the end of the experiments.

The fish used in the Series II experiments were acclimatized to water of 10°C. The long-photoperiod fish had been subjected to a total of 2240 hr (140 days) of light and 1120 hr (140 days) of darkness when the experiments began and 2960 hr (185 days) of light and 1480 hr (185 days) of darkness

when the experiments ended. For comparison, the total hours of daylight from sunrise to sunset for the same period amounted to 1986 hr at the beginning of the experiments and 2333 hr at the end of the experiments.

Although there were considerable variations between compartments with all three light sources, the tendency in both Series I and Series II experiments was for the control and long-photoperiod fish to avoid the light sources, with the greater percentage occupying the "darker" compartments, farthest from the light (Fig. 4). Chi-square values based on the total numbers of fish in each compartment, with all observation periods combined, yielded P-values

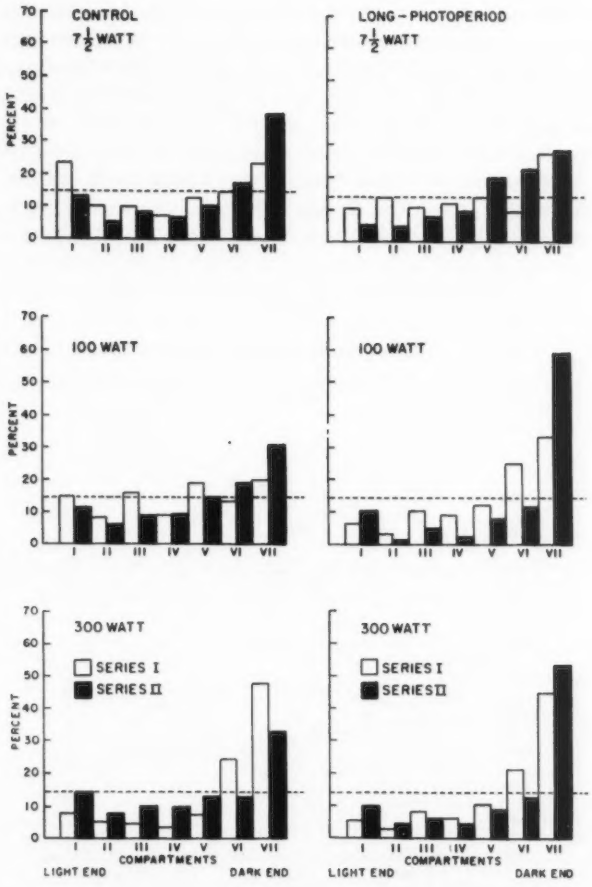


FIG. 4. Percentages of juvenile Atlantic salmon in each compartment of the horizontal light gradient tank with different light sources. The broken horizontal line represents the percentage expected in each compartment if random distribution existed.

less than 0.001 in each case indicating that this tendency to avoid the light sources was a very significant one. Except for the long-photoperiod fish in the Series I experiments with the 7½-w light, there was a greater percentage of control and long-photoperiod fish in compartment I than the adjacent compartment II with all three light sources in both Series I and Series II experiments (Fig. 4).

Because of variations between duplicate experiments and between observation periods in the same experiment, compartments I, II, III, and IV were combined and designated as Area A and compartments V, VI, and VII were combined and designated as Area B. A *t*-test on the proportions of fish in Area B was then used to compare the behavior of fish in the three light gradients.

There were no significant differences in the proportions of control fish in Area B with the 7½- and 100-w lamps in the Series I experiments (Fig. 5). However, in the Series II experiments, a significantly greater proportion of control fish was in Area B with the 7½-w than with the 100-w lamp, but the difference was not great, the *t*-value being only 2.78 ($P < 0.01$). In comparing the 100- and 300-w lamps, the significantly greater proportion of control fish was in Area B with the 300-w lamp in the Series I experiments whereas in the Series II experiments the greater proportion was in Area B

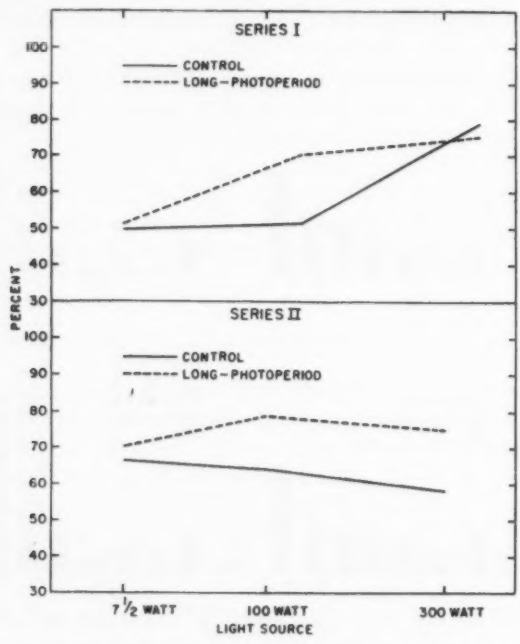


FIG. 5. Percentages of juvenile Atlantic salmon in Area B of the horizontal light gradient tank with different light sources.

with the 100-w lamp ($P < 0.001$ in each case). A comparison of the $7\frac{1}{2}$-w and 300-w lamps showed that a significantly greater proportion of fish was in Area B with the 300-w lamp in the Series I experiments whereas in Series II this occurred with the $7\frac{1}{2}$-w lamp ($P < 0.001$ in each case).

A comparison of the proportions of long-photoperiod fish in Area B with the $7\frac{1}{2}$-w and 100-w lamps revealed that a significantly greater proportion of fish occurred with the 100-w lamp in both the Series I and Series II experiments ($P < 0.001$ in each case) (Fig. 4). In comparing the 100-w and 300-w lamps the proportion of fish in Area B was significantly greater with the 300-w lamp in the Series I experiments ($P < 0.05$), but with the 100-w lamp in the Series II experiments ($P < 0.001$). A comparison of the $7\frac{1}{2}$-w and 300-w lamps revealed that the significantly greater proportion of fish in Area B occurred with the 300-w lamp in the Series I experiments but with the $7\frac{1}{2}$-w lamp in the Series II experiments ($P < 0.001$ in each case).

Comparisons between the proportions of control and long-photoperiod fish in Area B showed that, in the Series I experiments, there were no significant differences with the $7\frac{1}{2}$-w and 300-w lamps. With the 100-w lamp there was a significantly greater proportion of long-photoperiod fish in Area B ($P < 0.001$) (Fig. 5). In the Series II experiments there was a significantly greater proportion of long-photoperiod fish than control fish in Area B with the $7\frac{1}{2}$-w, 100-w, and 300-w lamps ($P < 0.001$ in each case) (Fig. 5).

Figure 6 shows the absence of either diurnal variations in behavior or uniform change in behavior with respect to length of time in the light gradients

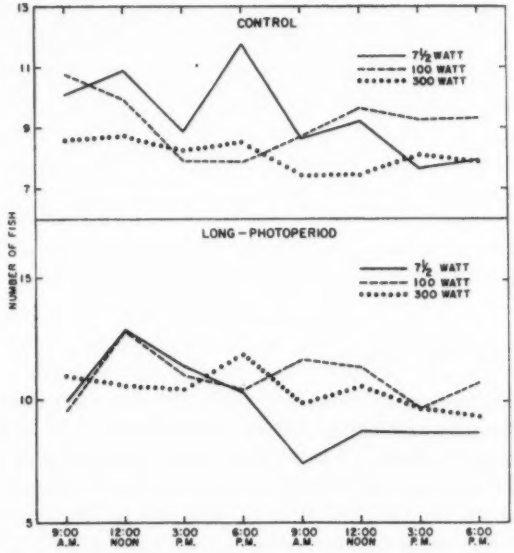


FIG. 6. Average numbers of juvenile Atlantic salmon in Area B of the horizontal light gradient tank at increasing time after the experiments began.

in the Series II experiments. The only indication of change in behavior with respect to length of time in the light gradient is with the 7½-w lamp but even in this case the trend is not very definite. The variations in Fig. 6 can for the most part be attributed to random wanderings and nipping and defence of territory on the part of the fish.

DISCUSSION

Vertical Light Gradients

Hoar (1951) states that fry of both pink salmon (*Oncorhynchus gorbuscha*) and chum salmon (*O. keta*) rise to the surface of the water at night under low light intensities. Also, coho smolts (*O. kisutch*) show a lower threshold of stimulation at night than coho fry and are much more active both day and night. Hoar (1953) states that coho and Atlantic salmon fry and steelhead trout (*Salmo gairdneri*) become inactive and sink to the bottom at night and this is a factor contributing to their prolonged stay in the streams. Hoar (1954) found that sockeye fry (*O. nerka*) showed more depth preference than any other species, whereas chum and coho fry were more evenly distributed in the water column. Sockeye smolts showed random distribution in deep water, whereas coho smolts were deeper in the water column. Hoar states that this behavior of sockeye smolts is believed to be one of escape rather than a light intensity reaction.

From a comparison of the results of the present study and the results of Hoar for Pacific salmon, it can be seen that the long-photoperiod fish, which became very active at low light intensities and swam toward the surface in a vertical water column, were similar in behavior to migrant species of chum and pink fry and coho and sockeye smolts. The control fish, which settled to the bottom at low light intensities and became quiescent, behaved much like the stages of coho and sockeye fry, which remain in the rivers and lakes.

The general conclusion is that the exposure of the Atlantic salmon fry to photoperiods resulted in the long-photoperiod fish being nearer the smolt stage of development and more active and sensitive to stimuli than the control fish. This caused them to rise toward the surface in a vertical water column at low light intensities, a behavior pattern very characteristic of migrant stages of Pacific salmon.

Horizontal Light Gradients

In all of the experiments in this study the fish were found to be photonegative, whether the intensity of the source of light was high (300-w lamp) or low (7½-w lamp). This is in agreement with the results found by Pinhorn and Andrews (1963), where the light source was directly above the water level and the stimulus was intermittent of 1-min duration in one case and a continuous light in another case. This seems to indicate, therefore, that the direction of the reaction of control and long-photoperiod juvenile Atlantic salmon is not greatly affected by the direction of the incident light.

Woodhead (1956) found that minnows (*Phoxinus phoxinus*) showed negative phototaxis in a horizontal light gradient, with an experimental apparatus similar to the one used in this study. Jones (1956) found a similar result with *Phoxinus phoxinus* using an experimental set-up similar to that used by Pinhorn and Andrews (1963). These experiments agree very well with the results found for juvenile Atlantic salmon in this study.

There were differences between the Series I and Series II experiments in avoidance reactions of the fish to the three light sources. Although the reasons for these differences were not investigated thoroughly, there are several possible reasons for them. They are: differences in acclimatization temperatures in the two groups of experiments, differences in time of exposure to the controlled photoperiods, differences in methods of observation, differences in ages and sizes of fish used, and differences in frequency of nipping and defence of territory. In our opinion the differences in frequency of nipping and defence of territory is the chief cause of the differences in the behavior of fish in the two groups of experiments.

Although aggressive behavior was not studied in detail, it was noted generally that nipping and defence of territory occurred more frequently in the Series II than in the Series I experiments. Stringer and Hoar (1955) have shown that the frequency of nipping and defence of territory increases with an increase in light intensity. If this were so in the present experiments the fish would be more randomly distributed at the higher light intensities and the apparent avoidance reaction would be greater for lower light sources than for higher light sources. This seems to explain the situation for control fish but long-photoperiod fish do not conform to this pattern in the lowest light gradient ($7\frac{1}{2}$-w). However, from the vertical light gradient experiments, the long-photoperiod fish showed increased activity at the lower light intensities; the results for long-photoperiod fish with the $7\frac{1}{2}$-w lamp may have been modified in this respect, so that the increased activity caused fewer numbers to remain in the darker areas of the tank because of random swimming to and fro. This would result in an apparent lesser avoidance of the $7\frac{1}{2}$-w light source.

Woodhead (1956) found results with *Phoxinus phoxinus* similar to those found in the Series I experiments. They showed a greater avoidance of the higher light sources in a horizontal light gradient.

The results of the horizontal light gradient experiments indicated that there was a tendency for the percentage of both control and long-photoperiod fish in compartment I nearest the light source to be greater than the percentage in compartment II. This may be a light-seeking tendency on the part of a certain proportion of the fish, but it is more likely due to bias in the experimental design such that the fish in the end compartments have only one escape route while those in other compartments have two.

Figure 5 indicates that the reactions of the control fish in the Series I experiments were similar under the $7\frac{1}{2}$-w and 100-w light sources whereas the reactions of the long-photoperiod fish were more alike under the 100-w

and 300-w light sources. This means that the long-photoperiod fish showed an avoidance reaction near their maximum with a lower light source than the control fish, between 7½ and 100w for this type of apparatus. The corresponding light source for the control fish was between 100 and 300w. In the Series II experiments the reaction was modified by nipping and defence of territory. Although this was not studied in detail, qualitative observations indicated that the frequency of nipping and defence of territory was greater with the control fish than with the long-photoperiod fish. This would cause the proportion of long-photoperiod fish in the "darker" Area B to be greater than the proportion of control fish with each light source because the control fish would be displaced more into the brighter areas than the long-photoperiod fish. This is believed to be the situation in the Series II experiments. In fact, as suggested by Pinhorn and Andrews (1963) and the vertical light gradient experiments in the present paper, if the long-photoperiod fish are actually physiologically nearer the smolt stage of development than the control fish, a decrease in the frequency of nipping and defence of territory is probably to be expected on the part of the long-photoperiod fish. Hoar (1951) states that the coho smolts nip and defend territory less frequently and less vigorously than the coho fry.

The differences that were apparent between the behavior of control and long-photoperiod fish in these horizontal light gradient experiments were believed to have resulted from the exposure to controlled photoperiods of the long-photoperiod fish causing them to be more active and sensitive to the light sources and physiologically nearer the smolt stage of development.

SUMMARY

1. In vertical light gradients the control fish exhibited a negative phototaxis at all light intensities studied. The long-photoperiod fish also exhibited a negative phototaxis at all light intensities except the lowest intensity where there was a tendency to move into the upper, more-lighted areas of the light gradient.
2. In vertical light gradients the long-photoperiod fish were very active at all light intensities studied and swam into the upper reaches of the water column at low light intensities. The control fish were less active at all light intensities studied and settled to the lower reaches of the water column at low light intensities.
3. The long-photoperiod fish showed maximum activity and greatest numbers in the surface layers of the vertical water column at 0.04 ft-c whereas the control fish showed this behavior at 1.0 ft-c.
4. In horizontal light gradients except for the fish nearest the light source both the control and long-photoperiod fish exhibited a marked negative phototaxis, avoiding the brighter areas of the tank with all light sources used.

5. Both control and long-photoperiod fish showed a stronger avoidance of light sources of higher intensity than of light sources of lower intensity in the Series I experiments. This trend was essentially reversed in the Series II experiments by nipping and defence of territory.
6. In the Series I experiments the reactions of the control and long-photoperiod fish were similar with the $7\frac{1}{2}$-w and 300-w light sources whereas the long-photoperiod fish showed the greater avoidance reaction with the 100-w light sources. Nipping and defence of territory modified the reactions in the Series II experiments such that the long-photoperiod fish showed a greater avoidance reaction than the control fish.

ACKNOWLEDGMENTS

The authors are indebted to Mr V. Hodder for aid in the statistical analyses, to Messrs A. W. May, R. Wells, and A. R. Murray for the critical reading of the manuscript, and to Messrs H. Mullett for the drafting and E. L. Rowe for the photography.

REFERENCES

HOAR, W.S. 1951. The behaviour of chum, pink and coho salmon in relation to their seaward migration. *J. Fish. Res. Bd. Canada*, **8**(4): 241–263.
1953. Control and timing of fish migration. *Biol. Rev.*, **28**: 437–452.
1954. The behaviour of juvenile Pacific salmon, with particular reference to the sockeye (*Oncorhynchus nerka*). *J. Fish. Res. Bd. Canada*, **11**(1): 69–97.

JONES, F.R.H. 1956. The behaviour of minnows in relation to light intensity. *J. Exp. Biol.*, **33**: 257–270.

PINHORN, A.T., AND C.W. ANDREWS. 1963. Effect of photoperiods on the reactions of juvenile Atlantic salmon (*Salmo salar* L.) to light stimuli. *J. Fish. Res. Bd. Canada*, **20**(5): 1245–1266.

STRINGER, G.E., AND W.S. HOAR. 1955. Aggressive behavior of underyearling Kamloops trout. *Canadian J. Zool.*, **33**: 148–160.

WOODHEAD, P.M.J. 1956. The behaviour of minnows (*Phoxinus phoxinus* L.) in a light gradient. *J. Exp. Biol.*, **33**: 257–270.

Survival of Lobsters, *Homarus americanus*, out of Water[1]

By D. W. McLeese

Fisheries Research Board of Canada
Biological Station, St. Andrews, N. B.

ABSTRACT

Median resistance times (MRT) in moist air at 0, 5, 10, and 15°C were determined for lobsters acclimated at 0, 10, and 20°C. At temperatures above 4–8°C depending on acclimation, there was an inverse relationship between median resistance time and temperature. A break in the relationship occurred at 4–8°C and further lowering of temperature to 0°C had no effect on MRT. Survival time was not increased by continuous sprays of sea water. Exposure to an air–oxygen mixture containing 40% oxygen by volume had no effect; however, lobsters died faster at 55–85% oxygen. Fed lobsters died faster than starved ones. An inverse relationship between MRT and metabolic rate was indicated.

INTRODUCTION

Lobsters for marketing alive are held out of water for periods from a few hours up to several days. Successful shipment can best be assured by knowledge of the facts pertaining to survival of lobsters out of water. Chaisson (1932) reported that air temperatures between 0.5 and 14°C were equally favourable for lobsters for 6 days. McLeese (1958) found that lobsters remained in good condition longer at 1.5°C than at 7°C. This paper reports on the resistance of lobsters taken from water at 0, 10, and 20°C and held in moist air at various constant temperatures and describes the effects of sprays of sea water, various air–oxygen mixtures, and of feeding.

MATERIALS AND METHODS

Test Animals

Hard-shelled lobsters ranging from 23–26 cm total length from tip of rostrum to tip of telson were obtained from a commercial supplier and held in the laboratory in fibreglass tanks supplied with flowing, aerated sea water. Those to be acclimated at 0°C and at 10°C were obtained when the local seawater temperature approximated these temperatures. Prior to testing, they were held in the laboratory in water at 0–2°C and at 10 ± 1°C for 2 days to 3 weeks. Those for 20°C acclimation were obtained in late summer when water temperature was approximately 15°C. They were held for a minimum of 3 weeks at 20 ± 1°C. Since McLeese (1956) found that lobsters acclimate to a temperature increase of 9°C in 3 weeks, the animals were considered to be fully acclimated to 20°C.

Lobsters were not fed with the exception of those used in feeding tests.

[1]Received for publication September 1, 1964.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

METHODS

SURVIVAL IN MOIST AIR. Groups of lobsters (usually 50) were exposed to moist air at temperatures of 0, 5, 10, and 15°C to determine their survival times. Lobsters were considered dead when no movement of any of the appendages could be detected even after gentle prodding. Temperature, relative humidity, and mortality were recorded daily.

Lobsters were tested in a cold room or in an insulated refrigerated chest. In the cold room, they were placed in fibreglass containers of 0.5 m^2 bottom area with no more than 25 individuals per container. To protect the lobsters from draughts and to maintain relative humidity at 90–100%, the containers were covered with sheets of wet, corrugated cardboard. To prevent contact with the cooling surface in the chest, lobsters were placed on a wooden platform $3\frac{1}{2}$ inches above the floor. Dampened cheesecloth draped over the walls maintained relative humidity at 90–100%. The air was gently circulated with a small fan to prevent temperature stratification and the chest lid was kept slightly open to maintain normal levels of oxygen and carbon dioxide.

SURVIVAL IN SPRAYS. Groups of 10 or 25 lobsters held in screen-bottomed trays in the cold room were sprayed with 30‰ sea water at rates of 0.1–120 litres/hr. The trays confined the groups of 10 lobsters to areas ranging from 0.05–0.25 m^2 and the group of 25 to 0.40 m^2. The heavier sprays were produced by passing sea water through perforated plastic tubing while the finer, mist-like sprays were produced with a spray gun or an air diffuser stone.

SURVIVAL IN OXYGEN–AIR MIXTURES. Oxygen was first bubbled through sea water to ensure a high relative humidity and then passed over 10 or 45 lobsters, in groups of 10, 15, and 20, in closed containers provided with exhaust vents to prevent pressure increase within the containers. By regulating the flow of oxygen, air–oxygen mixtures averaging 40, 55, 70, 75, or 85% oxygen by volume were obtained. Fluctuations seldom exceeded ±10 for 40, 55, and 85% oxygen or ±15 for 70 and 75% oxygen. Compressed air was passed through the containers for the tests at 21% oxygen. Oxygen and carbon dioxide were measured with a Fry gas analyser (Fry *et al.*, 1949). The containers were opened daily for observations, consequently, carbon dioxide did not accumulate for more than 1 day.

SURVIVAL OF FED VS. STARVED LOBSTERS. Groups of 10 or 25 lobsters were fed daily for 4, 5, or 10 days before exposure to moist air. The last feeding occurred shortly before they were removed from water. Each lobster was given 15 g of herring daily, of which approximately half was eaten. Lobsters starved for at least 3 weeks were used as controls. To determine if short periods without food would change survival time, groups of 10 lobsters were starved for periods up to 10 days.

TREATMENT OF THE DATA. The times to 50% mortality or the MRTs were read from plots of percentage mortality against time on logarithmic probability paper with the lines fitted by eye. As an example, data for 0°C acclimated groups are shown in Fig. 1. The MRTs are 8.5, 7.2, and 2.8 days

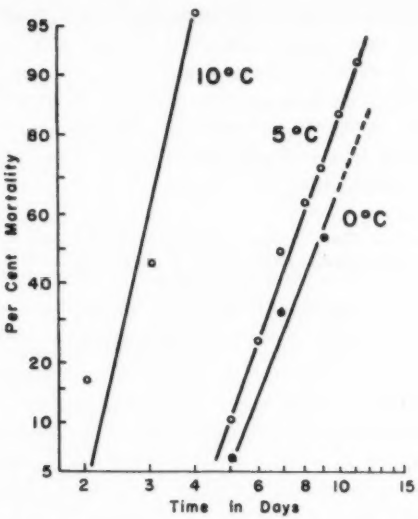


FIG. 1. Cumulative percentage mortality for groups of 50 lobsters acclimated at 0°C exposed in moist air at 0, 5, and 10°C. Plotted on probit × logarithmic axes.

for 0, 5, and 10°C tests, respectively. Confidence limits of 95% for the MRTs and the slopes of the lines were obtained by methods of analysis given in Litchfield (1949). To test whether the responses of two groups of lobsters were the same (95% probability), the MRTs and slopes were compared by methods given in Litchfield (1949) and Litchfield and Wilcoxon (1949).

RESULTS

MRTs IN MOIST AIR

Median resistance times and slopes together with their 95% confidence limits are listed in Table I. The slopes, which express rate of dying, vary from 1.2–1.75. Although it might be expected that slope could vary in relation to acclimation or test temperature, no consistent pattern was detected in these results.

Of the three tests at 5°C for lobsters acclimated at 10°C, the 8.0-day MRT determined in 1960 is significantly less than either the 10.2-day (1961) or the 11.0-day (1962) MRT. Although the difference cannot be explained, the 8-day MRT is considered to be aberrant. Where results from other treatments (spray, air–oxygen mixtures, food) were compared with those in moist air, within-year comparisons were made wherever possible. It was not necessary to use the aberrant 8.0-day MRT for any of the comparisons.

The response of the groups acclimated at a particular temperature was significantly different at the various test temperatures except for the 0 and

5° tests at 10°C acclimation. The 0°C tests differed in slope from the 10.2-day MRT at 5°C, but did not differ from the 11.0-day MRT at 5°C. The MRTs are plotted in Fig. 2 with the lines fitted by eye. Survival times (MRTs) increase as air temperature decreases to about 4, 8, and 4°C for acclimation temperatures of 0, 10, and 20°C, respectively. The slopes of the resistance lines change sharply at these temperatures and further lowering of air temperature does not increase survival time.

TABLE I. Median resistance times (days) and slopes for lobsters in moist air at various temperatures, previously acclimated in sea water at 0, 10, and 20°C. 95% confidence limits given in parentheses.

	Air temperature (°C)			
	0	5	10	15
0°C acclimation				
MRT	8.5 (7.6–9.5)	7.2 (6.6–7.8)	2.8 (2.6–3.0)	...
Slope	1.40(1.25–1.55)	1.30(1.25–1.40)	1.20(1.15–1.25)	...
No.	50	50	50	...
10°C acclimation[a]				
MRT	10.0 (8.5–11.8)	8.0 (7.0–9.0)	7.5 (7.0–8.1)	2.4 (2.2–2.7)
Slope	1.75(1.55–2.0)	1.50(1.35–1.65)	1.30(1.25–1.35)	1.50(1.40–1.65)
No.	50	50	50	50
MRT	10.5 (8.5–11.8)	10.2 (9.5–11.0)	...	...
Slope	1.70(1.50–1.95)	1.30(1.25–1.35)	...	...
No.	50	50	...	...
MRT	...	11.0 (9.7–12.4)	...	...
Slope	...	1.50(1.38–1.63)	...	...
No.	...	40	...	...
20°C acclimation				
MRT	13.0 (11.5–14.7)	10.5 (9.3–11.8)	5.8 (5.4–6.2)	2.6 (2.3–2.9)
Slope	1.40(1.25–1.55)	1.45(1.30–1.60)	1.25(1.20–1.30)	1.50(1.40–1.60)
No.	40	38	45	45

[a]For 10°C acclimation, tests with groups of 10 lobsters gave MRTs of 2.2 days at 15.6°C and 0.9 day at 18.3°C.

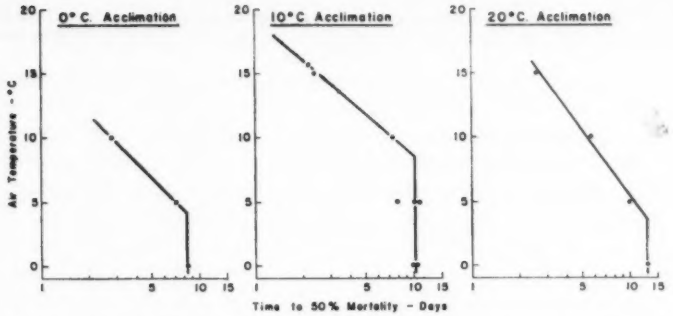


FIG. 2. Median resistance times at various air temperatures for lobsters acclimated at 0, 10, and 20°C. 0 — MRTs from Table I.

Except for the 5 and 15°C tests for 10 and 20°C acclimations, the responses of the groups tested at a particular temperature were significantly different for the various acclimation temperatures. The groups acclimated at the higher temperatures tended to have longer MRTs. The line for 20°C acclimation falls between the lines for 0 and 10°C acclimation over the range 5–15°C air temperature. At 0°C, however, 20°C acclimated lobsters lived longer in moist air than those acclimated at the lower temperatures. This is unlike their response to water temperature where those acclimated at high temperatures are less resistant to low water temperatures (McLeese, 1956). A possible explanation is presented in the discussion.

Survival in Sprays of Sea Water

MRTs and slopes from the various tests with sprays are listed in Table II. The slopes which range from 1.25–1.8 do not vary in a consistent pattern. From the seven tests at 5°C, two MRTs did not differ significantly from the corresponding MRTs for lobsters in moist air (Table I), one MRT was longer, and four MRTs were significantly shorter. There are no tests in moist air that correspond to those in sprays at 7.4 and 12.5°C but all four MRTs were on the left of the resistance lines (Fig. 2). Sprays did not extend survival out of water.

Survival in Air and Air–Oxygen Mixtures

MRTs and slopes from the tests are listed in Table III. Within this series of tests, the range in slopes, from 1.3 to 1.5, was small. Exposure to 21 and 40% oxygen gave MRTs that were not different from that for lobsters in moist air (Table I — MRT of 10.2 or 11.0 days). The MRTs from the four tests at 55–85% oxygen were significantly less. Exposure to air–oxygen mixtures did not extend survival out of water; rather exposure to 55–85% oxygen appeared to shorten survival.

Carbon dioxide, measured daily before the containers were opened, averaged 0.7% with a range of 0–3.5% within the containers at 21 and 40% oxygen.

TABLE II. Median resistance times (days) and slopes for lobsters in seawater sprays at various temperatures, previously acclimated in sea water at 0, 10, and 20°C. 95% confidence limits given in parentheses.

Rate of spray	Area sprayed	Acclimation temperature	Lobsters	Median resistance time	Slope
litre/hr	m^2	°C	*no.*		
5°C tests					
120	0.40	0	25	7.8 (6.1–9.9)	1.8* (1.5–2.2)
1.0	0.25	10	10	13.0 (10.5–16.0)	1.4 (1.2–1.6)
0.04	0.22	10	10	8.5*(7.5–9.6)	1.25*(1.1–1.4)
0.1	0.05	10	10	6.6*(5.3–8.2)	1.4 (1.2–1.6)
0.2	0.05	10	10	6.6*(5.3–8.2)	1.4 (1.2–1.6)
2.0	0.05	10	10	7.2*(6.1–8.4)	1.3 (1.1–1.5)
1.0	0.25	20	10	7.8 (6.8–9.8)	1.45 (1.2–1.7)
7.4°C test					
18	0.25	0	10	3.6 (2.8–4.6)	1.4 (1.2–1.8)
12.5°C tests					
5–10	0.15	10	10	1.3 (0.9–1.8)	1.7 (1.3–2.1)
30	0.15	10	10	1.5 (1.2–1.8)	1.4 (1.2–1.6)
100	0.15	10	10	1.5 (1.2–1.8)	1.4 (1.2–1.6)

*Differs significantly (95% probability) from the response in moist air at the same acclimation and test temperatures (Table I).

Since the results were the same as that for lobsters in moist air where there was no increase in carbon dioxide, it appears that carbon dioxide did not measurably affect survival.

In the tests at 75 and 85% oxygen, carbon dioxide averaged 0.7% with a range of 0–1.7%. In those at 55 and 70% oxygen, the average was 2.4% CO_2 with a range of 0–6.6%. The only significant difference was between the MRT of 6.6 days for 55% oxygen and the MRT of 8.0 days for 85% oxygen. The data do not show that 2.4% CO_2 affected the lobsters differently than 0.7% CO_2.

It has been shown that oxygen uptake by lobsters is considerably less in air than in water at the same temperature. McLeese (1964) found an average uptake of 8.4 ± 1.3 cc/kg/hr for lobsters in 6°C air. McLeese and Lisk (unpublished data) found an average of 17.9 ± 4 cc/kg/hr for those in 6°C water. Thomas (1954) reported values of 6–7 cc/kg/hr in 6°C air and 12–20 cc/kg/hr in 6°C water for the European lobster (*Homarus vulgaris*). The follow-

ing tests show that oxygen uptake in air–oxygen mixtures containing 60–80% oxygen by volume is comparable to uptake in water.

Groups of five lobsters were sealed in each of four plexiglass cylinders containing air and air–oxygen mixtures with 21, 60, 70, and 80% oxygen, respectively. The gas space inside each container was approximately 5.3 litres. A CO_2 absorbent (5 g tris (hydroxymethyl) aminomethane dissolved in 500 cc of sea water) was added to two other cylinders each with five lobsters and with 60 and 75% oxygen, respectively. The gas space in these was 4.8 litres. All six cylinders were kept at 5°C in the cold room for 52 hr. Over this period, 6–9 gas samples were withdrawn from each of the containers and the percentages of oxygen and carbon dioxide were determined. The decrease in oxygen and increase in carbon dioxide followed linear relationships in respect to time. The average rates of oxygen uptake were calculated from the volumes of oxygen taken up over the test period. Of the 30 lobsters in these tests, 27 became weak during testing, and only 6 recovered after return to sea water.

Regardless of the initial oxygen content, the lobsters took up 40–50% of the available oxygen in 48 hr. The average rate of oxygen uptake (Fig. 3) was directly proportional to the initial O_2 concentration when there was no CO_2 absorber.

In the containers without an absorber, CO_2 ranged from 3.4–8.9% in the tests at 21–80% oxygen, respectively. In those with the absorber (60 and 75% oxygen), CO_2 was apparently reduced to 4.0 and 3.8% but the rates of oxygen uptake remained high. Accordingly, initial oxygen content was the main factor causing the high rates of oxygen uptake although CO_2 may have been a contributing factor.

TABLE III. Median resistance times (days) and slopes for lobsters in air and in various air–oxygen mixtures at 5°C, previously acclimated at 10°C. 95% confidence limits given in parentheses.

Treatment	Lobsters	Median resistance time	Slope
% oxygen	*no.*		
21 (air)	45	10.0 (9.0–11.0)	1.4 (1.3–1.5)
21 (air)	10	10.2 (8.4–12.5)	1.3 (1.1–1.6)
40	10	10.8 (8.7–13.4)	1.4 (1.2–1.7)
55	45	6.6*(6.0–7.2)	1.3 (1.2–1.4)
70	45	7.0*(6.3–7.9)	1.5*(1.4–1.6)
75	10	7.6*(6.3–9.2)	1.4 (1.2–1.6)
85	45	8.0*(7.4–8.6)	1.3*(1.2–1.4)

*Differs significantly (95% probability) from the response in moist air at the same acclimation and test temperatures (Table 1).

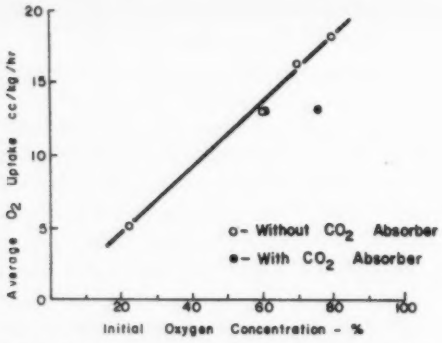


FIG. 3. Average oxygen uptake by lobsters in sealed containers at 5°C in relation to initial oxygen concentration.

The rates of uptake of 13–18 cc/kg/hr at 60–80% oxygen at 5°C (Fig. 3) approximate the values for uptake in water at 6°C. However, the MRTs from the survival tests at 55–85% oxygen were shorter than in moist air which suggests a possible inverse relationship between metabolic rate and MRT.

MRTs of Fed and Starved Lobsters

MRTs and slopes from the various tests with fed and starved groups are listed in Table IV. In all seven cases, the MRTs of fed and recently fed (starved 1 day) groups were shorter than MRTs of those starved for 3 weeks. In five cases the differences were significant. Feeding shortens survival time out of water. For no apparent reason, the MRTs for the fed (15 days) and starved control (16 days) for 10°C acclimated lobsters exposed at 5°C both exceeded the 10.2-day MRT for those in moist air (Table I).

In the two series where lobsters were starved for various periods, there was no apparent increase in MRT for starvation periods longer than 2 days.

DISCUSSION

Since keeping lobsters wet with sprays did not extend their survival out of water, it appears that drying of the gills is not a cause of death in moist air. The trend towards shorter survival times as air temperature increases above 4–8°C depending on acclimation suggests there may be an inverse relationship between metabolic rate and survival time out of water. Lobsters acclimated at 10°C had longer MRTs at air temperatures above 5°C than those acclimated at 0 or 20°C. Possibly the 10°C acclimated groups were under less environmental stress because they are near the middle of the temperature range normally encountered in nature. At that acclimation they can be active over a wider range of temperatures than at other acclimation temperatures (McLeese and Wilder, 1958).

TABLE IV. Median resistance times (days) and slopes for lobsters in moist air, previously fed or starved for various periods and acclimated at 10 or 20°C. 95% confidence limits given in parentheses.

Treatment	Acclimation temperature	Lobsters	Median resistance time	Slope
	°C	no		
5°C tests				
Fed 10 days	10	25	15.0*(12.2–18.5)	1.7*(1.4–2.0)
" 5 "	10	25	6.6*(5.9–7.4)	1.4 (1.2–1.6)
Starved 1 day	10	10	8.5*(7.2–10.0)	1.3 (1.2–1.5)
" 2 days	10	10	9.6 (7.7–12.0)	1.4 (1.2–1.6)
" 4 "	10	10	9.2 (7.9–10.7)	1.3 (1.1–1.5)
" 5 "	10	10	10.0 (9.0–11.2)	1.2*(1.1–1.3)
" 10 "	10	10	10.0 (9.0–11.2)	1.2*(1.1–1.3)
" 21 "	10	25	10.0 (9.1–11.0)	1.3 (1.2–1.4)
" 21 "	10	25	16.0*(13.0–19.5)	1.7*(1.4–2.0)
10°C tests				
Fed 10 days	10	10	3.7*(3.2–4.2)	1.2 (1.1–1.4)
" 4 "	10	10	3.5*(2.9–4.3)	1.4 (1.2–1.5)
Starved 1 day	10	10	4.7*(4.1–5.3)	1.2 (1.1–1.4)
" 2 days	10	10	6.6 (5.4–8.1)	1.4 (1.2–1.6)
" 4 "	10	10	7.8 (6.5–9.5)	1.3 (1.2–1.4)
" 5 "	10	10	6.6 (5.7–7.9)	1.2 (1.1–1.3)
" 10 "	10	10	6.6 (5.4–8.1)	1.4 (1.2–1.6)
" 21 "	10	10	6.6 (5.3–8.2)	1.4 (1.1–1.7)
Fed 4 "	20	10	2.4*(1.9–3.2)	1.5*(1.2–1.6)
Starved 21 "	20	10	3.6*(2.8–4.6)	1.5*(1.2–1.6)

*Differs significantly (95% probability) from the response in moist air at the same acclimation and test temperatures (Table I).

As previously pointed out, 20°C acclimated lobsters survived longer at 0°C air temperature than those acclimated at either 0 or 10°C. The temperature drop from 20 to 0°C would probably reduce their metabolism to a lower rate than that for lobsters from 0 or 10°C. It is possible, then, that their longer

MRT at 0°C could be related to a lower metabolic rate induced by this drastic decrease in temperature.

More oxygen was consumed when lobsters were exposed to mixtures of air and oxygen, presumably reflecting an increased metabolic rate. They died more rapidly at 55–85% oxygen.

Recently fed lobsters died faster than starved lobsters which suggests a relationship between MRT and metabolic rate. Bramsnaes and Boëtius (1953) with the European lobster, and McLeese (1964) with the American lobster showed that metabolic rate, as measured by their oxygen uptake, almost doubled after feeding.

The complete series of tests indicates that there is an inverse relationship between metabolic rate and survival time of lobsters in moist air.

ACKNOWLEDGMENTS

Much of the work was carried out during the summers of 1959–1962 with the capable assistance of Misses Eileen Stiven (1959), Nora Young (1960), and Susan Corey (1961 and 1962). Mrs F. Willa Williamson and Mr U. J. Walsh assisted at other times.

REFERENCES

Bramsnaes, F., and J. Boëtius. 1953. Storage of live lobsters. Meddelelse fra Fiskeriministeriets Forsøgslaboratorium, pp. 1–16, November 1953. [FRB Translation Series No. 63.]

Chaisson, A. F. 1932. Factors in the shipment of live lobsters from eastern Nova Scotia. *Bull. Biol. Bd. Canada*, No. 33, 29 pp.

Fry, F. E. J., A. C. Burton, and O. G. Edholm. 1949. A simple gas analyzer. *Canadian J. Res. E*, **27**: 188–194.

Litchfield, J. T., Jr. 1949. A method for rapid graphic solution of time-per cent effect curves. *J. Pharmacol. Exp. Therap.*, **97**: 399–408.

Litchfield, J. T., Jr., and F. Wilcoxon. 1949. A simplified method of evaluating dose-effect experiments. *J. Pharmacol. Exp. Therap.*, **96**(2): 99–113.

McLeese, D. W. 1956. Effects of temperature, salinity and oxygen on the survival of the American lobster. *J. Fish. Res. Bd. Canada*, **13**(2): 247–272.

1958. Air shipment of lobsters. *Dept. of Fisheries of Canada, Trade News*, **10**(9): 5–6.

1964. Oxygen consumption of the lobster, *Homarus americanus* Milne Edwards. *Helgolaender Wiss. Meeresuntersuch*, **10**(1–4): 7–18.

McLeese, D. W., and D. G. Wilder. 1958. The activity and catchability of the lobster (*Homarus americanus*) in relation to temperature. *J. Fish. Res. Bd. Canada*, **15**(6): 1345–1354.

Thomas, H. J. 1954. The oxygen uptake of the lobster (*Homarus vulgaris* Edw.). *J. Exp. Biol.*, **31**(2): 228–251.

Changes in a Stream Population of Trout Associated with Increased Silt[1]

By J.W. Saunders and M.W. Smith

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

ABSTRACT

Low standing crops of brook trout, *Salvelinus fontinalis*, were closely associated with silting in Ellerslie Brook, Prince Edward Island, and appeared to result from the destruction of hiding places. Spawning was also curtailed by silting. Following scouring, trout stocks soon increased. The remarkable adaptability of trout to silting, in a habitat with favourable flow and water temperature, was illustrated.

INTRODUCTION

The many spring-fed streams on Prince Edward Island are highly productive of brook trout (*Salvelinus fontinalis*) (Smith, 1951). The underlying rock formation of the province is, for the most part, Permo-Carboniferous red sandstone. Podzols are the dominant group of well- and moderately-well-drained soils (Whiteside, 1950). These soils are readily eroded. In consequence, following rains most streams run "red" with suspended silt eroded from farm lands, chiefly potato fields, and from deep ditches that drain unsurfaced roads.

Within the drainage basin of Ellerslie Brook, Prince Edward Island, in recent years soil erosion by water has been on the increase. It was particularly severe during the autumn of 1958 and in the following spring when the lower 2000 yards (1 yard = 0.9144 m) of the brook received an unusually heavy burden of silt from the ditches of a newly repaired road (Fig. 1). About 250 yards of stream were silted over throughout the summer of 1959 and remained so until autumn when the silt was scoured away by freshets.

Annual assessments of the summer standing crops of trout in Ellerslie Brook were made since 1951. This was part of a study to determine the effects of pond formation on anadromous fish (Smith and Saunders, 1958). The present paper deals with the effects of erosion silt on the distribution and numbers of brook trout in Ellerslie Brook with emphasis on observations made when part of the stream was silted up during the summer of 1959.

THE ELLERSLIE SYSTEM

Ellerslie Brook is a small spring-fed stream with a length at low-summer levels of about 6 miles (1 mile = 1.61 km). The stream has been described (Smith and Saunders, 1958). The drainage area is approximately 10 square

[1]Received for publication September 25, 1964.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

miles (26 km^2), of which about 1800 acres (730 ha) are under cultivation. Top soils in the drainage area are a permeable sandy loam (Smith, 1959).

A dam built in 1952 forms a 5-acre (2-ha) pond near head of tide (Saunders, 1960). The brook flows into Malpeque Bay on the north shore of Prince Edward Island. The geography and hydrography of the estuary have been described (Needler, 1931, 1941; Saunders and Smith, 1964).

Mean annual precipitation in the area is about 40 inches (1 inch = 2.54 cm). The brook is subject to freshets, particularly in autumn and in spring. Water discharge from the stream has varied from less than 1, at low-summer levels, to over 345 ft^3/sec (1 ft^3 = 0.0283 m^3) when the brook was in unusually heavy spate (Smith and Saunders, 1958).

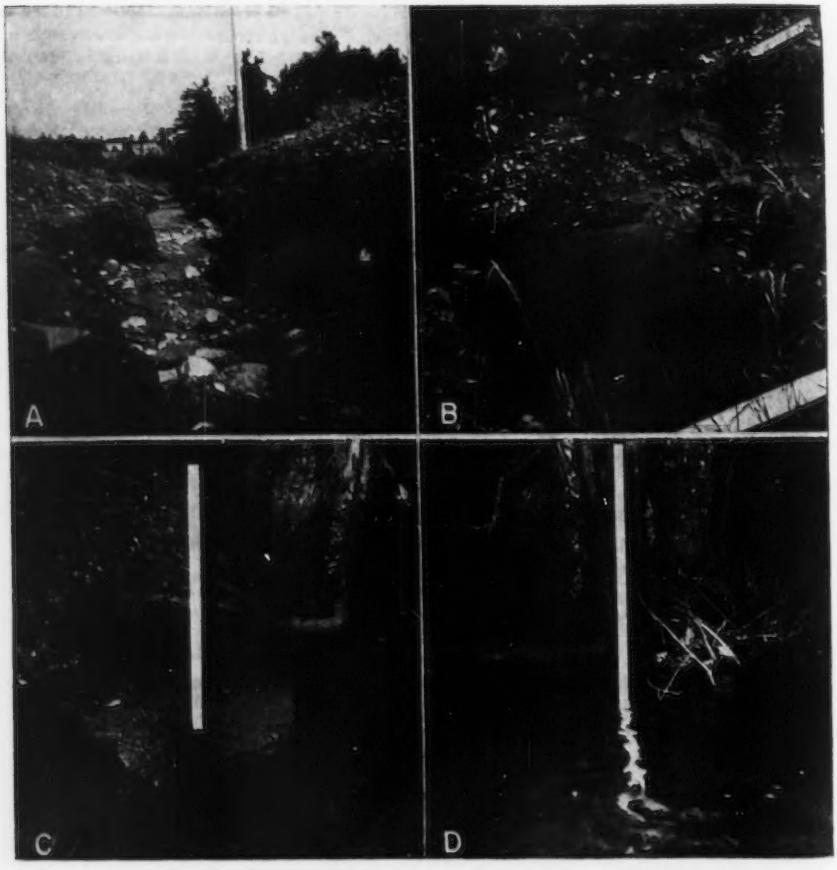


FIG. 1. Erosion and silting on Ellerslie Brook, P.E.I. A. Road ditch as source of silt. B. Silt at junction of ditch and brook. C. Pool choked with silt. D. Same pool in following year after scouring.

For this paper, a road which crosses Ellerslie Brook about 2000 yards above its mouth has been set arbitrarily as the boundary between the lower and upper reaches of the brook.

Erosion Silt

As Wickett (1959) points out, there are various standard systems for the classification of silt. At Ellerslie Brook all sediment carried into the stream was designated as silt, notwithstanding that particle size varied from coarse gravel down to very fine clay. Cultivated farm lands and rural roads, most of them unsurfaced, are the chief sources of silt in the Ellerslie drainage area.

Cultivated land. Some time prior to 1950 about a mile of the upper reaches of Ellerslie Brook was silted over. The silt was eroded from nearby potato fields. As pointed out by Ripley *et al.* (1961), potatoes are a very poor soil-conserving crop. Some of the potato fields were converted into pasture land in 1951 and in following years; subsequently the grass cover reduced erosion in that part of the drainage area. However, much of the stream there is still silted over.

At present four fields that border the stream just above the road that marks the boundary between the upper and lower brook appear to be the principal sources of agricultural silt in the system. Potatoes have been grown in one or more of these fields during each year since 1955.

Rural roads. Roads cross the brook and its tributaries at five different places. All contribute silt to the lower brook. In addition, drains (tap drains) that carry water away from low-lying places in road ditches were opened into the lower brook in 1956 and 1957.

Erosion is most severe following road repairs that involve the removal of the protective cover of vegetation from the ditches. Such was the case when heavy rains during the autumn of 1958 and in the following spring changed the ditches of a newly repaired road (the boundary road, see above) into deep gullies (Fig. 1). Throughout the summer of 1959, about 250 yards of the brook, downstream from the road, were heavily silted over and remained so until the autumn when the silt was scoured away. The area silted over contained a 50-yard study section (section A) in which the fish population had been assessed annually since 1951. Silt was also observed in most of the pools in the lower brook during the summer of 1959.

Measurement of silt. There are no data relative to the annual silt load in Ellerslie Brook. But some idea of this may be gained from the deposition of silt on the pond bottom since it was formed in the autumn of 1952. Average depth of silt over the pond in the summer of 1963 was 3 ft. In some places, depths to 5 ft or more were encountered. Collectors held on the pond bottom over a number of years showed that deposition was greatest in the period from autumn to spring. Whiteside (1950) attributed heavy erosion in autumn and spring to the fact that rains were heavy at a time when the land was usually bare or sparsely covered with vegetation.

POPULATION ASSESSMENTS

Assessments of the summer standing crops of trout in the same (usually 12) 50-yard study sections in Ellerslie Brook and in a 450-yard section in the tributary, Hayes Brook, have been made annually since 1951. Fish were captured by electrofishing. Repeated tests have shown that this is an effective way to capture trout in the hard water of Ellerslie Brook (Saunders and Smith, 1954). Age determinations were not made, but from the grouping of the length frequencies of Ellerslie trout, it was possible to classify trout smaller than 8 cm as fingerlings (age 0).

Fingerlings were marked by removal of the adipose fin. Trout older than age 0 (the majority were yearlings, age 1) were tagged with serially numbered jaw tags (Smith, 1957). Fork lengths (tip of snout to fork in tail) were recorded in centimetres.

EFFECTS OF SILTING

On the Distribution of Trout

The distribution of trout in relation to different habitat types was studied in section A for a number of years. While the section was silted over during the summer of 1959, it was possible to observe the effects of silt on the distribution of trout in this section in comparison with that in previous years with little silt.

In 1959, depths of silt in section A varied from 1 inch to 2 ft or more, with an average of 4 inches (based on 40 measurements). The only pool in the section was filled in (Fig. 1). Small, silt-free patches were found behind rocks where turbulence systems kept the stream bottom clear. Also silt-free was a narrow rectangular space, 6 × 1 ft across the stream, at the head of a former riffle. Over most of the section water depths were not in excess of 2 inches. Ripple marks on the surface of the silt were similar to those commonly seen on sand beaches.

In the years before section A was silted over, fingerlings (age 0) were found under or near rocks throughout a flat water area and on the riffle. Most of the older trout (1+ and older) were found in the pool. A few, less than 10% of the older trout in any year, were found in association with debris in flat water areas.

A marked change was noted in the distribution of trout after the section was silted over. Fingerlings were found only in the silt-free space at the head of the riffle where small rocks provided cover. Older trout were found on the small patches of clean bottom behind rocks, sometimes as many as three trout were on the same patch. This association of trout with clean patches of bottom was also observed in a 500-yard section of another Prince Edward Island stream that was polluted by sawdust. There, older trout, and a few fingerlings, were found by electrofishing only in a sawdust-free area at the head of a riffle in a type of habitat where older trout are not commonly found. Deep (5 ft or more) pools with sawdust accumulations on the bottom were barren of trout. Otherwise, such pools would typically be occupied by older trout.

Possibly trout were attracted to patches of clean bottom not only because they were relatively free of silt but also by the turbulence systems that kept those areas clear. Another possibility is that the clear areas provided feeding places. However, Tarzwell (1937) showed that sand bottoms produced few invertebrates. Tebo (1955) observed a reduction in stream invertebrates after silting.

On Standing Crops of Trout

Assessments of annual summer (August and early September) standing crops of trout in section A are summarized in Table I and illustrated in Fig. 2. Standing crops in nine other 50-yard study sections in the lower brook, downstream from section A, and one (section B) on the headwaters are presented in Fig. 2.

Data gathered after 1961 are not reported herein since a stream improvement program, begun on Ellerslie Brook in 1962, involved a number of the study sections. This program was similar to one reported for the tributary, Hayes Brook (Saunders and Smith, 1962).

In the lower brook. Standing crops of trout in section A and in the nine study sections downstream from it fell from a general high in 1955 to near record lows in 1959 (Table I, Fig. 2). One of the factors that contributed

Table I. Summer standing crops of trout in section A that was silted over in 1959 (mean fork length of trout in centimetres in parentheses).

Year	Numbers of trout		
	Fingerlings, age 0	Age 1 and older	Total
1951	100 (6.6)	39 (13.5)	139
1952	184 (6.2)	56 (12.5)	240
1953	147 (6.2)	81 (11.2)	228
1954	126 (6.6)	46 (12.0)	172
1955	160 (6.1)	70 (11.4)	230
1956	132 (6.6)	56 (12.0)	188
1957	106 (6.7)	23 (10.8)	129
1958	74 (6.7)	33 (12.3)	107
Means	129±33 (6.5±0.2)	51±18 (12.0±0.8)	179±47
1959 (year of silting)	40 (6.8)	16 (11.9)	56
1960	96 (6.6)	26 (13.2)	122
1961	103 (6.8)	40 (11.1)	143

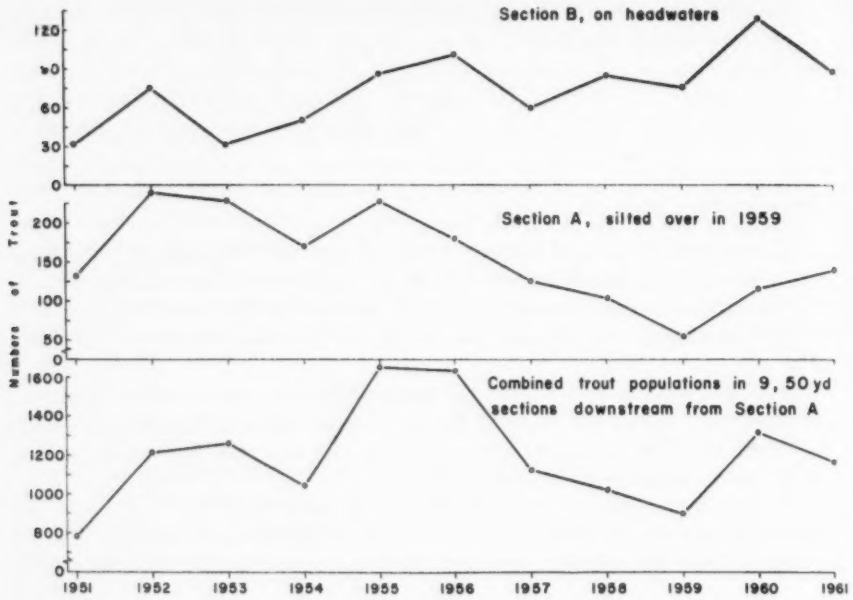


FIG. 2. Fluctuations in numbers of brook trout in Ellerslie Brook, 1951–61.

to this decline was silting, which was unusually heavy in the lower brook from 1955 through 1959. The association of silting with low standing crops was apparent in the lower brook during the summer of 1959 when silting was severe in that area.

There were 33 older trout in June 1959 in the silted area (60 yards long) between the road which was heavily eroded in 1958–59 and the head of section A. In August 1957, 167 fingerlings and 152 older trout were captured in the area.

The standing crop in section A in 1959 was the lowest on record (Table I). The percentage drop in 1959 from the averages of the numbers in the 8 years preceding the heavy silting was the same (70%) for both fingerlings and older trout. Downstream from section A in the nine study sections where there was less silt, standing crops of fingerlings and older trout in 1959 were 25% below the averages in the previous years. The greatest depressions in population densities occurred in the sections that contained pools which were silted over. In many instances undercuts along the banks of those pools were filled with silt. In other years trout were observed to occupy undercuts as favoured habitats. Thus, low populations in some years were strongly associated with loss of suitable trout habitats, particularly hiding places, through silting. In a previous study in the Ellerslie tributary, Hayes Brook, it was observed that the constancy in the numbers of hiding places was reflected in the relative

constancy in the numbers of older trout in the annual standing crops (Saunders and Smith, 1955).

In the upper brook. Whereas the population trend in the lower brook was downward from 1955 through 1959, the trend in section B, on the headwaters of Ellerslie Brook, has been moving upward since 1952 (Fig. 2). The upward trend in section B is attributed to the abatement of soil erosion on nearby farm land following the conversion of much of the cultivated land into pasture land in 1951 and in subsequent years. When the first assessment of section B was made in 1951 the area was choked with silt, and according to reports from local farmers had been in that condition for some time. With time much of the silt was scoured away and the banks became undercut in a number of places. The undercuts were quickly utilized by older trout as they were formed. After silt was scoured away from riffles a marked improvement was also noted in fingerling stocks.

On Spawning

The view that silting in streams is injurious to spawning grounds is commonly accepted (Herbert *et al.*, 1961; Wickett, 1959). The extent to which silting curtailed spawning in Ellerslie Brook is not known. There were no fingerling trout in the heavily silted, 60-yard section of stream immediately above section A in June 1959; some were there, however, in August, indicating movement into the area. Under favourable conditions the area was known to be productive of fingerlings; 167 were found there in 1957 when there was little silt. Possibly the fingerling population in section A in 1959 (Table I) may have also represented fish that had moved into the section before the August assessment. Herbert *et al.* (1961) concluded that brown trout in polluted (by china-clay wastes) reaches of a Cornish stream had migrated from the clean headwaters.

On Survival of Trout

All (74) of the fingerlings in section A in the summer before it was silted over (1958) were marked by removal of the adipose fin; 32 (one escaped) of the 33 older trout received a numbered jaw tag. None of the fin-marked or tagged trout was recaptured in the section in 1959. Fingerlings could not be identified once out of the section. Of the 32 tagged trout, three were angled in other parts of the system in 1959, one was recaptured in section A in 1960, the remainder (28) were not seen again.

The poor carry-over of 1958 stocks in section A to the same area the next year could have resulted from heavy mortalities among the 1958 stocks or from movement out of the section, or from both. The possible harmful effects of the direct action of suspended silt on trout were not investigated in Ellerslie Brook. Herbert and Merkens (1961) suggest that even low concentrations of suspended solids might potentiate other stresses in the environment which were not severe enough to produce more than a negligible mortality. They

stress that their results, which were obtained in aquaria, might not be applicable to natural environments. As Cordone and Kelley (1961) point out, "the fact remains that little data are available to support any universal answer, on whether or not sediment is directly harmful to fish."

In view of the fact that water turbidity is a common occurrence in Ellerslie Brook, as it is in most Prince Edward Island trout streams, it is difficult to view suspended solids as anything more than a minor factor contributing to fish mortalities in the Ellerslie system.

On Size of Trout

Lengths of older trout in section A in 1959 were slightly below the averages observed for previous years in this section (Table I). Possibly the slight decrease in size is attributable to silt. It should be kept in mind, however, that since the 1959 stocks in section A were recruited from some other part of the stream prior to the August assessment it is possible that they had not been in section A long enough to have their growth affected by silt.

On the average, older trout were larger (12.7 cm) in the nine downstream sections in 1959 than in section A (11.9). The average length of older trout in the nine sections in 1959, however, was within the length range (11.7–13.7) encountered in the sections in the years prior to 1959. Herbert *et al.* (1961) attributed normal growth of brown trout in a stream polluted by china-clay wastes to the fact that the trout fed to a considerable extent on terrestrial forms.

RECOVERY FROM SILTING

The scouring away of silt from a stream habitat in Ellerslie Brook was usually followed by a rise in its trout-carrying capacity. This was demonstrated in section B on the headwaters (Fig. 2).

Heavy freshets during the winter of 1959–60, and in the following spring, scoured away a good part of the silt that was observed in the lower brook during the summer of 1959. Silting was light in the lower brook in 1960 and in subsequent years. This was due in large part to the growth of vegetation in the ditches of the road that was rebuilt in 1958, and between the stream banks and fields cultivated for potatoes in the vicinity of the middle section of the brook. It is also possible that erosion was greatest when the fields were first cultivated after having existed as meadows. With the absence of heavy silting in 1960 and 1961, population remained at a good level throughout the Ellerslie system (Fig. 2).

All of the evidence at hand supports a conclusion that when silting is temporary its harmful effects on brook trout are not lasting, if as in Ellerslie Brook, other factors such as flow and temperature of water are favourable for the species.

SUMMARY

Silting and low standing crops of brook trout were closely associated in Ellerslie Brook, Prince Edward Island. The observed reductions in stocks

appeared to have been brought about through the destruction of habitats which were suitable for trout, chiefly hiding places. Silt also exercised harmful effects on spawning. The effect of silt through direct action on trout was an unknown factor. However, considering the fact that water turbidity is a common occurrence in the stream its direct effects are considered to be small. There was some evidence that unusually heavy silting affected the size of trout. Following scouring the trout-carrying capacities of affected areas increased, and there were no lasting effects from silting. The fact that brook trout were able to retain a foothold in those habitats that were silted over is evidence of the remarkable ability of the species to cope with certain adverse conditions, in this case silt, in the environment when other environmental conditions are favourable.

Over the years the gradual sedimentation of erosion silt, chiefly from cultivated land, has destroyed a good portion of the upper part of Ellerslie Brook as a brook trout habitat. Salt marshes (formed by sedimentation of silt brought in from the sea and land) on the upper parts of the estuary at Ellerslie and on other streams in Prince Edward Island have markedly reduced trout habitats in those estuarial areas. There is no reason to suppose that the destruction of trout habitats in the Ellerslie system will not continue.

ACKNOWLEDGMENTS

Assistance in the field of C.R. Hayes and Earl Coughlin and in the laboratory of Miss Mary Holmes and D.K. Rushton is gratefully acknowledged.

REFERENCES

CORDONE, A.J., AND D.W. KELLEY. 1961. The influences of inorganic sediment on the aquatic life of streams. *California Fish and Game*, **47**(2): 189–228.

HERBERT, D.W.M., AND J.C. MERKENS. 1961. The effect of suspended mineral solids on the survival of trout. *Int. J. Air. Wat. Poll.*, **5**(1): 46–55.

HERBERT, D.W.M., J.S. ALABASTER, M.C. DART, AND R. LLOYD. 1961. The effect of china-clay wastes on trout streams. *Ibid.*, **5**(1): 56–74.

NEEDLER, A.W.H. 1931. The oysters of Malpeque Bay. *Bull. Biol. Bd. Canada*, No. 22, 35 pp.

1941. Temperatures and salinities under the ice in a shallow inlet. *J. Fish. Res. Bd. Canada*, **5**(3): 236–243.

RIPLEY, P.O., WM. KALBFLEISCH, S.J. BOURGET, AND D.J. COOPER. 1961. Soil erosion by water. *Canada Department of Agriculture, Research Branch, Publication* 1083, 34 pp.

SAUNDERS, J.W. 1960. The effect of impoundment on the population and movement of Atlantic salmon in Ellerslie Brook, Prince Edward Island. *J. Fish. Res. Bd. Canada*, **17**(4): 453–473.

SAUNDERS, J.W., AND M.W. SMITH. 1954. The effective use of a direct current fish shocker in a Prince Edward Island stream. *Canadian Fish Culturist*, No. 16, pp. 42–49.

1955. Standing crops of trout in a small Prince Edward Island stream. *Ibid.*, No. 17, pp. 32–39.

1962. Physical alteration of stream habitat to improve brook trout production. *Trans. Am. Fish. Soc.*, **91**(2): 185–188.

1964. Planting brook trout (*Salvelinus fontinalis* (Mitchill)) in estuarial waters. *Canadian Fish Culturist*, No. 32, pp. 25–30.

SMITH, M.W. 1951. The speckled trout fishery of Prince Edward Island. *Canadian Fish Culturist*, No. 11, pp. 1–6.

1957. Comparative survival and growth of tagged and untagged brook trout. *Ibid*, No. 20, pp. 1–6.

1959. Phosphorus enrichment of drainage waters from farm lands. *J. Fish. Res. Bd. Canada*, **16**(6): 887–895.

SMITH, M.W., AND J.W. SAUNDERS. 1958. Movements of brook trout, *Salvelinus fontinalis* (Mitchill) between and within fresh and salt water. *J. Fish. Res. Bd. Canada*, **15**(6): 1403–1449.

TARZWELL, C.M. 1937. Experimental evidence on the value of trout stream improvement in Michigan. *Trans. Am. Fish. Soc.*, **66**: 177–187.

TEBO, L.B., JR. 1955. Effects of siltation, resulting from improper logging, on the bottom fauna of a small trout stream in the southern Appalachians. *Prog. Fish-Culturist*, **17**(2): 64–70.

WHITESIDE, G.B. 1950. Soil survey of Prince Edward Island. Experimental Farm Service, Charlottetown. 83 pp.

WICKETT, W.P. 1959. Effects of siltation on success of fish spawning. Proc. Fifth Symposium on Water Pollution Res. Pacific Northwest. Siltation — its sources and effects on the aquatic environment. U.S. Public Health Serv., Portland, Oregon, pp. 16–22 (mimeographed).

Respiratory Metabolism of Pumpkinseed (*Lepomis gibbosus*) in Relation to Swimming Speed[1]

By J. R. Brett and D. B. Sutherland

Fisheries Research Board of Canada
Biological Station, Nanaimo, B. C.

ABSTRACT

By use of a "tunnel" respirometer the relation between oxygen consumption (Y, mg O_2/kg/hr) and swimming speed (X, body lengths/sec) for 45-g pumpkinseed at 20°C was found to follow the equation $\log_{10} Y = 1.65 + 0.31\ X$. Standard and active metabolic rates were 45 ± 6.6 and 408 ± 39 mg O_2/kg/hr, respectively. Maximum 60-min sustained swimming speeds averaged 3.01 ± 0.27 lengths/sec.

At low velocities, with more than one fish present, elevation of the metabolic rate occurred from aggressive behaviour, reaching one-half the active rate.

INTRODUCTION

During studies on the relation of respiratory metabolism to swimming speed in young sockeye salmon, *Oncorhynchus nerka*, it was observed that the excitable nature of the fish resulted in considerable variability in the metabolic rate accompanying all but the highest speeds (Brett, 1964). In addition, there appeared to be a lower metabolic "plateau" which did not decline despite a decrease in the velocity of the water flowing through the respirometer. These observations left some doubt as to the nature of the overall relation between oxygen consumption and swimming speeds, and the reliability of extrapolation to zero velocity as an estimate of standard metabolism.

It was decided to test another species of fish reputed to be less excitable. For this purpose the pumpkinseed, *Lepomis gibbosus*, was chosen. Experiments were conducted at 20°C, a normal summer temperature for this species.

MATERIALS AND METHODS

Twelve pumkinseed were obtained on July 23 from Prospect Lake, near Victoria, B. C., and held for 1 month at $20 \pm .5$°C. Their mean total length and weight were 12.7 cm and 44.9 g, respectively. Experiments were conducted during September with one retest in December.

Determinations of metabolic rate in relation to swimming speed were made using the technique and apparatus described for young sockeye (Brett, 1964). In brief, fish were put into the "tunnel" respirometer at about 5 PM and left overnight with adequate exchange of water. A velocity of 0.1 ft/sec was maintained by recirculation. A series of early-morning readings on rate of oxygen consumption (Winkler determinations) was taken at this minimum

[1]Received for publication August 10, 1964.

J. Fish. Res. Bd. Canada, 22(2), 1965.
Printed in Canada.

velocity. The velocity was then increased in steps of 0.2 ft/sec, each step being maintained for 60 min, followed by a 15-min flushing period to re-establish oxygen level. Successive determinations of metabolic rate were made until a fatigue velocity was reached which exhausted the fish prior to the end of the 60-min period. A maximum 60-min sustained speed ("critical speed") was determined in the following manner. If the fish swam for 60 min at 1.1 ft/sec and fatigued during the next step at 1.3 ft/sec in 30 min the critical speed was: $1.1 + (30/60 \times 0.2)$ ft/sec = 1.2 ft/sec. In this way the final speeds were adjusted on a proportional basis.

This arbitrary determination was found to approximate the maximum sustained speed in experiments on sockeye yearlings when tested for 6 and 10 hr (Brett, 1964).

RESULTS

In the respirometer the pumpkinseed responded well but showed distinct restlessness at low velocities. Above velocities of about 1 length (L)/sec (approximately 0.4 ft/sec) there was a change in swimming behaviour from sculling with pectoral fins to propulsion with the caudal fin, frequently using a series of darts to maintain position. This behaviour was rarely accompanied by any over excitement such as fluttering or nosing the walls of the plexiglass tunnel.

In the hope of obtaining quiescence at low velocities, four fish of very similar size (range = 26.8–32.3 g) were tested together. Excellent behaviour was obtained above 1 L/sec. Below this velocity, with accompanying freedom of movement, intense aggression broke out in an unresolved competition for favoured positions. The data for this group are plotted in Fig. 1.

A straight line was obtained when the logarithm of rate of oxygen consumption was plotted against speed, except where energy was obviously dissipated in ways other than swimming directly into the current. The orderly relation of the data above 1 L/sec, when coupled with the observations on behaviour below this speed, provided support for the method of determining standard and active metabolism by extrapolation to the minimum (zero) and maximum sustained level of activity. Similar extrapolations to states of rest not obtained in the laboratory have been used where standard rates of metabolism were determined by use of activity meters (e.g. Beamish and Mookherjii, 1964).

Using the above approach, the balance of experimental fish was tested (Table I). Standard metabolic rate averaged 45 ± 6.6[2] mg O_2/kg/hr. Active metabolic rate was 408 ± 39 mg O_2/kg/hr at a 60-min fatigue swimming speed of 3.01 ± 0.27 L/sec (approximately 1.22 ft/sec). A re-run on fish No. 10, $2\frac{1}{2}$ months later and 0.7 g heavier, provided an almost identical record for comparable velocities.

DISCUSSION

The range of metabolic rate reported herewith is unusually large for a centrarchid, the active rate being approximately nine times the standard rate.

[2]Standard deviation.

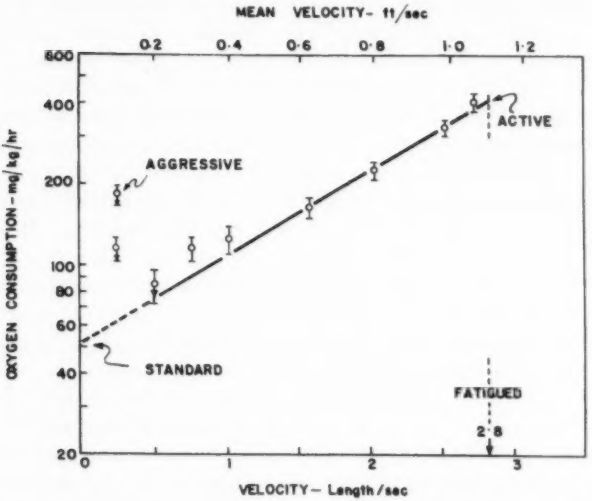


FIG. 1. Oxygen consumption and swimming speed of a group of four pumpkinseed averaging 11.9 cm and 30.2 g at 20°C. Accuracy of oxygen determinations is indicated by limits equivalent to ±0.04 ppm. Arrows indicate that a lower value would be expected because of observed restless behaviour.

TABLE I. Metabolic rate and critical swimming speed of pumpkinseed at 20°C. The maximum and minimum observed rates of oxygen consumption are included together with the derived active and standard levels (by extrapolation).

	Total length	Wet weight	Maximum O_2-consumption	Minimum O_2-consumption	Active metabolism	Standard metabolism	Critical swimming speed	
	cm	*g*	*mg/kg/hr*	*mg/kg/hr*	*mg/kg/hr*	*mg/kg/hr*	*ft/sec*	*L/sec*
Number	12	12	6	8	6	6	6	6
Mean	12.7	44.92	409	75	408	45	1.22	3.01
S.D.	.96	13.9	39	19.6	39	6.6	...	0.27
S.E.	.27	4.0	16	6.9	16	2.7	...	0.11
Fish No. 10								
Sept. 26/61	13.1	46.40	332[a]	58	430[b]	40	1.30	3.00
Dec. 12/61	13.2	47.10	433	59	430	40	1.32	3.07

[a]No higher reading taken (2.8 L/sec) but critical swimming speed recorded.
[b]Determined by extrapolation to critical speed.

It is of interest to compare these results with those reported for the bluegill, *Lepomis machrochirus*, by Wohlschlag and Juliano (1959). Applying their equations relating oxygen consumption to weight, temperature and swimming speed, standard values of 110 and 167 mg O_2/kg/hr are obtained for summer and fall seasons (at 20°C). Active rates range from 224 to 347 mg O_2/kg/hr, using the same maximum swimming speed obtained for pumpkinseed. At most these represent a capacity to elevate the resting metabolic rate by a factor of three times, which is in agreement with Fry's (1957) generalizations on respiratory metabolism for fish. Since Wohlschlag and Juliano report individual cases of active metabolic rate rising to 450 mg O_2/kg/hr, it is apparent that the greatest difference lies in the values for standard metabolism.

If the general equation[3] of Winberg (1961) relating standard metabolism and size for freshwater fish at 20°C is applied, a rate of 215 mg O_2/kg/hr is obtained. This is three times the *observed* minimum level for pumpkinseed and five times the *calculated* standard level. The pumpkinseed data therefore add confirmatory evidence for a lower level of standard metabolism than has generally been reported. Beamish (1964) and Beamish and Mookherjii (1964) came to similar conclusions for brown trout, brook trout, common white sucker, brown bullhead, carp, and goldfish.

A comparison with the O_2-*consumption rate vs swimming speed* of young sockeye of comparable weight (Brett, 1964) shows that the 20°C curve for the warm-water sunfish almost matches the 5°C relation for the cold-water salmon (Fig. 2). The ecological significance of the relative metabolic rates is apparent.

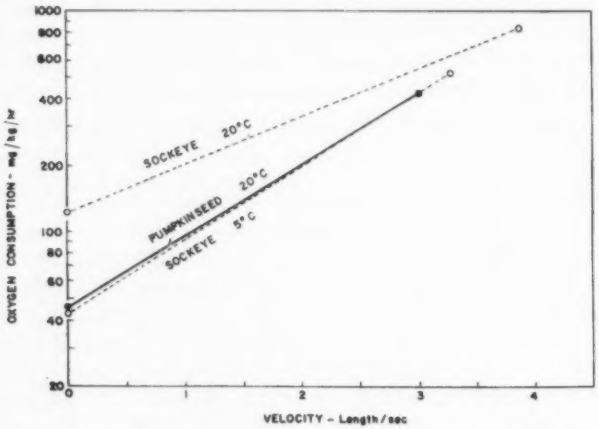


FIG. 2. Metabolic rates in relation to swimming speed for pumpkinseed and sockeye of approximately the same weight (*ca.* 50 g).

[3] $Y = 0.307\ X^{0.81}$, where Y = ml O_2/hr and X = weight in g.

CONCLUSIONS

The semilogarithmic expression relating O_2-consumption and swimming speed is a satisfactory linear transformation of the data. Truncation at low velocities can be ascribed to additional demands on metabolism from excitement.

The comparatively low level of standard metabolism obtained at 20°C for pumpkinseed is in keeping with similar observations on young sockeye at 5°C.

Aggressive behaviour among pumpkinseed may elevate metabolic rate to nearly one-half the active level.

ACKNOWLEDGMENTS

The fish were kindly supplied by Mr D. R. Hurn, Regional Biologist for the British Columbia Fish and Game Branch, Department of Recreation and Conservation.

REFERENCES

BEAMISH, F. W. H. 1964. Respiration of fishes with special emphasis on standard oxygen consumption. II. Influence of weight and temperature on respiration of several species. *Canadian J. Zool.*, **42**: 177–188.

BEAMISH, F. W. H., AND P. S. MOOKHERJII. 1964. Respiration of fishes with special emphasis on standard oxygen consumption. I. Influence of weight and temperature on respiration of goldfish, *Carassius auratus* L. *Canadian J. Zool.*, **42**: 161–194.

BRETT, J. R. 1964. The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd. Canada*, **21**(5): 1183–1226.

FRY, F. E. J. 1957. The aquatic respiration of fish, pp. 1–63. *In* M. E. Brown [Ed.], Physiology of Fishes, Vol. I. Academic Press Inc., New York.

WINBERG, G. G. 1961. New information on metabolic rate in fishes. *Voprosy Ikhtiologii*, **1**(1/18): 157–165. [Fish. Res. Bd. Canada, Translation Series No. 362.]

WOHLSCHLAG, D. E., AND R. O. JULIANO. 1959. Seasonal changes in bluegill metabolism. *Limnol. Oceanogr.*, **4**(2): 195–209.

Studies on the Quality of Newfoundland Cod. 10. Effect of Some Commercial Freezing Rates on the Frozen and Stored Quality of Trap Cod[1,2]

By W.A. MacCallum, Dorothy A. Chalker[3], and E.J. Laishley[4]

Fisheries Research Board of Canada
Technological Unit, St. John's, Nfld.

AND

W.J. Dyer and D.R. Idler

Fisheries Research Board of Canada
Technological Research Laboratory, Halifax, N.S.

ABSTRACT

Time–temperature curves are reported for points at the centre, one-quarter depth, and at the surface of blocks of dressed cod, and blocks and packages of cod fillets, frozen in commercial plate freezers. Freezing rates at the centres varied by a factor of about 4 where thickness of the pack was the only variable. The same factor applied to the fastest- and slowest-frozen fish in 4½-inch-thick blocks. Using a special arrangement, dressed trap-caught cod and cod fillets were then frozen, some at the fast rate and some at the slow rates normally encountered at the centre of 1¾- and 4½-inch-thick commercial packs, respectively (0.7 and 2.7 hr through the temperature range of 32 to 5°F (0 to −15°C)). The frozen and stored (at −10°F) samples were of similar quality for periods up to 22 weeks, based on taste panel assessment.

INTRODUCTION

Cooling curves developed by early workers, (e.g. Stiles, 1922; Weld, 1927) showed that the rate of freezing becomes slower as the depths of the fish are reached. MacKay and Weld (1926) and Weld (1927) observed larger ice crystals in the slower-frozen portions of cod than in the more rapidly frozen tissue. These findings were complemented by data which showed that greater amounts of drip were obtained from the more slowly frozen muscle (MacFayden, 1927; Weld, 1927). Scientists in the years following produced a body of work in which freezing rates applicable to the slowest-to-freeze portions of the pack are reported. Portions frozen at different rates within the same fish or package were not studied separately. Notevarp and Heen (1940) working with cod, and Young (1938, 1939) with Pacific salmon and halibut, found no great difference

[1]Received for publication September 11, 1964.
[2]Publications 1–7 inclusive in this series, not previously numbered, are listed in Appendix I of Paper No. 8 (MacCallum *et al.*, submitted to J. Fish Res. Bd. Canada).
[3]Present address: British Food Manufacturing Industries Research Association, Leatherhead, Surrey, England.
[4]Present address: Department of Biological Science, Purdue University, West Lafayette, Indiana.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

in quality resulting from slow and fast freezing as judged by the taste panel. Dyer (1951, 1953) found a greater decrease in extractable actomyosin in slow-frozen than in fast-frozen cod and haddock but concluded that such differences were soon overshadowed by the greater effects of storage temperature.

For an equally long period, other scientists were involved in analytical studies of the freezing process. Plank (1913, 1941) pioneered work on the prediction of freezing times at the centre of the slab, cylinder, sphere, and the rectangular parallelopiped. However there was practically no published data available on rates of freezing foodstuffs under *commercial* operating conditions (Lowe *et al.*, 1950). Long (1955) made a significant start on a program to remedy this situation. Others, including Nagaoka *et al.* (1955), Levy (1958), Eddie and Pearson (see Levy, 1958), Charm (1962), and Slavin (1964) made practical contributions to the calculation of freezing times at the centre of whole and packaged fish. Experimental data relating to slowest freezing rates under commercial conditions are still few, however. The present authors were interested in rates at points *other than the centre* of plate frozen blocks but none could be found.[5] It was decided therefore to record these data and to make a further study of the effect of the freezing rate variable. Unfavourable effects on the cold storage quality of fish frozen at the centre of a 4½-inch-thick pack in contrast to that at the centre of a 1-inch package could complicate the interpretation of data being gathered for other purposes.

Using post-rigor cod, Gutschmidt (1963) found decreased texture scores in very slowly frozen (15 hr in 32 to 5°F zone (0 to −15°C)) material after 3 months storage at 0°F (−18°C) over quick-frozen (20 min in 32 to 5°F zone) samples, though there was no difference immediately after freezing. Only the quick rate of freezing used by Gutschmidt was close to that found in better commercial practice. The present work includes a documentation of some of the different freezing rates associated with commercial practice and a taste-panel evaluation of pre-rigor material frozen at three rates which fall within the observed range. Potentially, pre-rigor material may be important to the trap fishery of Newfoundland and to Canadian operations involved in freezing at sea. In some instances trap landings in particular have been found to be susceptible to accelerated deterioration in quality in frozen storage (Dyer *et al.*, 1962; MacCallum *et al.*, unpublished data) and thus might be expected to show the effect of slow freezing. The point to be determined was whether the slowest *commercial* rate would prove to be sufficiently slow to produce observable deteriorative effects.

EXPERIMENTAL

Commercial Freezing Rates

In order to provide freezing curves, points at the surface and at one-quarter and mid-depths of the following commercial blocks and packages were

[5]For exception see Watzinger (1951) who monitored the temperature change with time at several points in blocks 3.3 inches in thickness.

monitored: (a) 85–95-lb blocks, $18 \times 36 \times 4\frac{1}{2}$ inches, of "dressed"[6] cod (*Gadus morhua*) frozen in an original Torry Hall vertical-plate freezer (Yule and Eddie, 1953); (b) 20-lb waxed paper cartons ($10\frac{3}{4} \times 21 \times 2\frac{3}{8}$ inches) of skinless cod fillets frozen in an Amerio Horizontal-plate freezer; (c) 1-lb waxed paper cartons ($3\frac{1}{8} \times 8\frac{5}{8} \times 1\frac{1}{8}$ inches) of skinless cod fillets frozen in the Amerio freezer. The freezing conditions used are specified in Fig. 1. Copper constantan thermocouples were used in conjunction with a multi-point recorder. The temperatures at the centre of three pre-rigor, $4\frac{1}{2}$-inch blocks of dressed fish of mixed sizes, ranging from 3 to 6 lb, were recorded. The surface, one quarter and mid points in each of two similar post-rigor frozen blocks of dressed fish of a similar range of sizes, in each of two post-rigor frozen $2\frac{3}{8}$- and 1-inch cartons of fillets and in each of two pre-rigor frozen 1-inch cartons of fillets were monitored. Fillet blocks and packages were placed in the freezing trays with those of regular plant production to ensure freezing at commercial rates. After

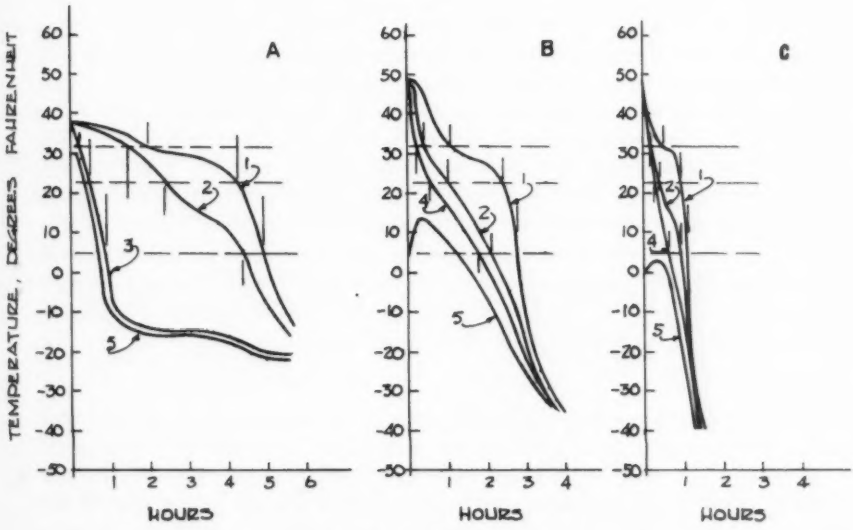


FIG. 1. Freezing curves for points in the fish and on the plates used for freezing blocks and cartons of cod. Location of thermocouple in blocks or packages, 1, geometric centre; 2, opposite 1 and mid-way between centre and surface; 3, opposite 1 and under fish skin at surface (of block); 4, opposite 1 and under carton cover at surface; 5, opposite 1 on refrigerated plate warmed by fish. Aluminum trays were used with the packs described under B and C. Hydraulic pressure was provided in the Amerio freezer to promote contact of cartons with freezing plates. Mechanical pressure was provided in the Torry-Hall freezer. **A.** Freezing $18 \times 36 \times 4\frac{1}{2}$-inch, 95-lb blocks of whole, eviscerated cod in an original Torry-Hall vertical-plate freezer flooded with ammonia at about −28°F (−33°C), gravity circulation. **B.** Freezing $10\frac{3}{4} \times 21 \times 2\frac{3}{8}$-inch, 20-lb waxed paper cartons of skinless cod fillets in an Amerio horizontal-plate freezer flooded with ammonia at about −45°F (−43°C), gravity circulation. **C.** Freezing $3\frac{1}{8} \times 8\frac{5}{8} \times 1\frac{1}{8}$-inch, 1-lb waxed paper cartons of skinless cod fillets under conditions described under B.

[6]Beheaded and gutted but not de-finned or trimmed at the nape.

freezing, the samples were thawed in air to a temperature of about 30°F and the positions of all temperature measuring points confirmed before results were plotted.

Freezing at Controlled Rates

FILLETS

Live cod, 20–30 inches long and at a temperature of 40°F, (4.5°C) were gutted and iced at a trap near St. John's in late June 1962. The fish were landed, washed, filleted, and skinned within 1½ hr of capture. The fillets were packed in 1-lb waxed paper cartons ($3\frac{1}{8} \times 8\frac{5}{8} \times 1\frac{1}{8}$ inches) and were overwrapped with waxed paper, separated into two lots, coded, and frozen pre-rigor. One station of a horizontal-plate freezer was filled with three layers of packages in order to obtain a slow rate of freezing (centre layer). The upper and lower layers comprised of 1½-inch-thick packages (Fig. 2a, bottom sketch) were discarded later. Seventeen $1\frac{1}{8}$-inch-thick, 1-lb cartons were slow-frozen in the centre layer for taste panel tests while others, similarly frozen, were fitted with copper-constantan thermocouple leads inserted in the centre of the cartons to determine the freezing rate (Fig. 2a). The time for freezing at the centre of the cartons of expendable fish was recorded as well. A strip chart multi-point recorder was used. In a second station of the freezer, twenty 1-lb cartons of the test fish were placed directly in contact with the freezer plates (Fig. 2a, upper sketch). Three of these cartons were fitted with thermocouple leads to permit data on fast freezing to be recorded (Fig. 2a).

After freezing, all cartons of fillets for taste-panel evaluation were packed in commercial cardboard cartons, which were sealed with masking tape, and the cartons were stored within a 4 × 4 × 3-ft insulated box and held in a commercial cold storage room at −10°F (−23°C).

WHOLE FISH

On the day following the preparation of the frozen fillets, other live fish 18–20 inches long were trapped in the same area. These fish, at a temperature of 45°F (6.7°C), were gutted and iced at the trap. Small fish of uniform size were required to permit satisfactory one-layer packing in the unfilleted state. The cod were landed, headed, washed, and packed in waxed paper cartons each measuring $10\frac{3}{4} \times 21 \times 2\frac{3}{8}$ inches thick and holding nine fish each. The nine cod were wrapped in paper in three lots of three to permit quick access to a portion of the pack at time of testing, thereby ensuring continuous storage at −10°F for all remaining samples. Eight cartons were prepared, four for fast and four for slow freezing in the pre-rigor state.

An arrangement similar to that described above was followed to provide slow-frozen samples while expendable fish fillets were used in the outer layers. The latter were in 1-lb packages ($1\frac{1}{8}$-inch thick) while the test fish, in the $2\frac{3}{8}$-inch-thick cartons, were in a layer between the 1-lb cartons (Fig. 2b, bottom sketch). Four composite packs, each of total thickness of $4\frac{3}{4}$ inches were frozen.

The inner and outer layers of the fourth pack were fitted with thermocouple leads to determine the freezing rate (Fig. 2b). The four composite packs were placed within a single station of the plate freezer. In a second station of the plate freezer four $2\frac{3}{8}$-inch-thick cartons of test fish were placed side by side, one carton deep, in direct contact with the freezer plates. One of the cartons (Fig. 2b, upper sketch) was fitted with thermocouples.

After freezing, the $2\frac{3}{8}$-inch-thick cartons of test fish were packed three to a cardboard carton, and the latter sealed with masking tape. All cartons were stored under conditions identical to those for the fillets.

Taste panel evaluation of the baked samples followed the procedures of Dyer and Dyer (1949), modified for frozen fish. Samples were baked, examined for texture, taste, and odour and scored principally on the basis of the first two qualities with more weight given to texture. Scores are reported on a scale of 0–100. Best quality fish score 80–90; those samples which score below 40 are below the level of acceptability of the analytical panel.

RESULTS AND DISCUSSION

Commercial Freezing Rates

Too few blocks were frozen to permit an assessment of the effect of packing density on freezing rate. The centres of the three $4\frac{1}{2}$-inch blocks of pre-rigor dressed cod and the two of post-rigor material (average packing density 53 lb/ft^3), were lowered through the critical zone (32 to 23°F) at the rate shown by the curve in Fig. 1. The similarity of freezing rates for pre- and post-rigor

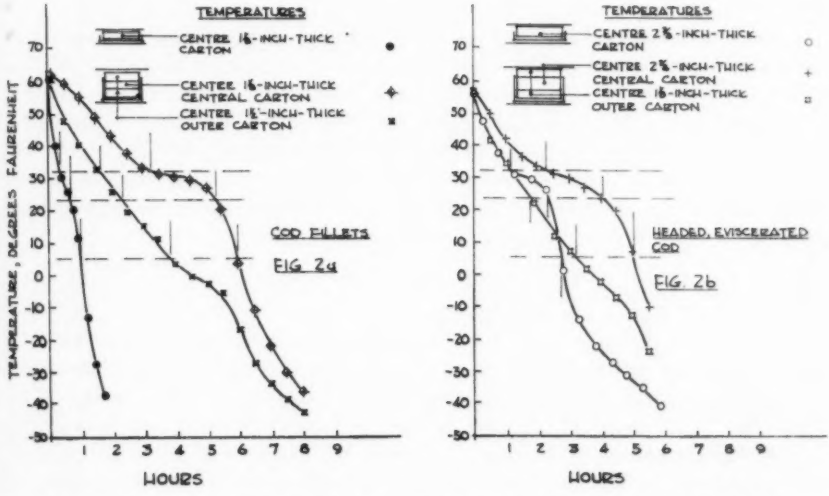


FIG. 2. Freezing curves for cod packed in waxed paper cartons. Aluminum trays were used without lids. Hydraulic pressure provided firm contact of freezing plates with cartons in the commercial Amerio horizontal-plate freezer used. The plates were flooded with ammonia at about −45°F (−43°C), gravity circulation.

material is in agreement with results reported by Merritt and Templeton (1963). Similarly packed cartons of pre-rigor and post-rigor fillets (average packing density of 64 lb/ft^3) were frozen at approximately the same rates. These are illustrated by the remaining typical curves in Fig. 1. It is evident that samples representative of quite different freezing rates may be found within any one pack, but particularly within the 4½-inch block. The flesh at the centre of this block was 2.2 hr in the critical zone. This was 2.5 times and 11 times longer, respectively, than that required for flesh at the one-quarter point and at the surface of the block to drop in temperature from 32 to 23°F. At least half the total weight of fish in the 85–95-lb blocks was lowered through the critical zone in from 10 to 40% of the time taken for flesh at the centre of the block to pass through the same range. Merritt and Templeton (1963) have reported a reduction of at least 1 hr from the above freezing times for fish at the centre of 4-inch blocks frozen between extruded aluminum plates of a vertical-plate freezer refrigerated to −40°F. Despite this technical advance it is still necessary to hold blocks of 4-inch thickness in the freezer for considerably longer periods than required for the thinner fillet cartons in order to achieve the same low temperatures at the centre of the pack.

The flesh at the centre of the 4½-inch blocks dropped from 32 to 5°F (0 to −15°C) in 2¾ hr as compared to 0.7 hr for the fillets at the centre of the 1-lb pack. Thus commercially frozen dressed and filleted fish may be frozen at rates varying by a factor of at least 4 where thickness of the pack is the only variable. A similar factor of 4 applies to freezing times required to lower the flesh at extreme positions within a 4½-inch-thick block (at the centre and at the surface) through the same temperature zone.

The fish used for freezing were fairly warm. For the described conditions and equipment, freezing times through the critical zone are probably close to minimal values. Long (1955) showed that time through the critical zone may be reduced as much as one-half under identical plant-operating conditions if freezing is commenced using warm fish, rather than fish at 32°F. Nevertheless, the starting temperatures shown in Fig. 1b and 1c are higher than would be recommended for commercial handling, and freezing times for fish chilled below 40°F prior to freezing would be increased slightly.

Freezing at Controlled Rates

The term "freezing rate" requires comment. The present authors follow certain common practices and state freezing rate as the longest time spent in a specific temperature zone, e.g. the critical zone (32 to 23°F) or the 32 to 5°F (0 to −15°C) zone. The former is preferred since this is the zone in which greatest change occurs in amount of water frozen (Dyer *et al.*, 1957). However, as is evident from Fig. 1b and 1c, when anything but the rate of freezing at the centre is concerned, the temperature change at this level is so rapid that the range 32° to 5°F gives a more practical measure of actual freezing rate and therefore sometimes has to be used in practice. Another definition (Kondrup

and Boldt, 1960) expresses the freezing rate as the ratio of one-half the thickness of pack divided by the time required to lower the temperature at the centre through the chosen zone. In current work on whole fish (Fig. 2b) the times required for flesh at the centre of $4\frac{3}{4}$- and $2\frac{3}{8}$-inch-thick packs to be lowered from 32 to 5°F were by the former definition 2.7 and 1.6 hr (Table I), respectively, and by the latter definition 2.2 and 1.9 cm/hr, respectively. Freezing times (from 32 to 5°F) for fillets in the centre of $4\frac{1}{8}$- and $1\frac{1}{8}$-inch-thick packs

TABLE I. Results of taste panel evaluation of trap cod samples frozen in various times corresponding to commercial conditions.

Storage (−10°F; −23°C) time in weeks	Texture[b]	Taste	Overall acceptability
Whole, headed, eviscerated cod			
		Freezing time[a]: 2.7 hr	
5	80±(5.6) 18	73±(3.9) 18	77±(5.2) 18
12	82±(3.8) 15	79±(4.8) 15	82±(3.8) 15
15	79±(5.7) 15	74±(4.4) 15	80±(4.2) 15
22	90±(2.6) 23	73±(3.5) 23	83±(2.3) 23
		Freezing time: 1.6 hr	
5	77±(4.2) 18	71±(2.1) 18	77±(3.0) 18
12	74±(4.9) 15	81±(6.2) 15	79±(2.5) 15
15	83±(4.0) 15	69±(6.4) 15	79±(4.6) 15
22	78±(2.4) 23	72±(3.5) 23	74±(4.1) 23
Cod fillets		Freezing time[a]: 2.7 hr	
$\frac{1}{2}$	73±(4.8) 20	76±(5.2) 20	73±(4.8) 20
12	85±(2.9) 15	79±(2.3) 15	83±(3.3) 15
15	77±(6.3) 15	74±(4.8) 15	75±(6.5) 15
22	69±(6.7) 24	76±(3.7) 24	73±(4.9) 24
		Freezing time: 0.7 hr	
$\frac{1}{2}$	91±(2.7) 20	86±(3.8) 20	89±(2.6) 20
12	84±(3.1) 15	70±(6.3) 15	79±(3.7) 15
15	88±(5.0) 15	75±(5.0) 15	83±(4.5) 15
22	78±(4.3) 26	72±(3.5) 26	74±(4.1) 26

[a]Time for lowering temperature through range 32 to 5°F (0 to −15°C).
[b]Average values are shown followed by the standard error of the mean (in parentheses) and by the number of judgments.

(Fig. 2a) were 2.7 and 0.7 hr (Table I), respectively, while by the latter definition they were almost identical for the two packs, 1.9 and 2.0 cm/hr, respectively. Thus, when freezing conditions are described for both shallow and deep packs exposed to the same freezing potential, the rate expressed as hours spent in a particular temperature zone provides a clearer comparison of conditions than does freezing rate defined in centimetres/hour units. In uniform freezing from two sides the slowest freezing rate, expressed by either definition, is always associated with freezing at the centre of the pack; thus results reported below and in Table I refer to slowest rates and maximum times. Maximum rates and minimum times may be estimated by referring to Fig. 1.

Initial quality of all frozen samples was fairly high (Table I), but results show a rather large variation. On freezing, the difference in texture scores of the fast- and slow-frozen *fillets* was significant (5% level) but this was not the case in the stored samples. No significant difference in quality between fast- and slower-frozen *round fish* was observed. This condition was maintained throughout the whole period of storage with the exception of the 22-week samples. In the latter instance, the slow-frozen pack was just significantly better (5% level). In general, results on the effect of freezing rate are in agreement with other work. Some early workers (see Introduction), and Kondrup and Boldt (1960) in their review of the effect of freezing rate on frozen meat and poultry, and Dyer and Dingle (1961) in a similar review for fish, had indicated that little influence of the freezing process over a wide range of freezing rates could be detected, other than in appearance.

Thus the analysis of the present data showed clearly that the panel could not detect significant differences between the slower- and faster-frozen samples held in storage for up to 22 weeks at −10°F. Similarly, the large variation found prevents any conclusion relative to the possible changes because of pre-rigor freezing. While these results by no means preclude the possibility that subtle differences might be detected should other means of assessment be used, the results indicate that little difference may be expected in the market condition of trap cod of high initial quality frozen at any of these commercial rates and package thicknesses and stored at −10°F. Results are reassuring in view of the necessity, from the practical and engineering viewpoint, to resort to fairly thick blocks in handling dressed frozen fillets and unfilleted fish (MacCallum and Ellis, 1964; MacCallum *et al.*, 1964). Moreover, the performance of commercial freezers is not always up to par (MacCallum, 1955; subsequent unpublished data). Freezing rates of the order of the slowest commercial rate reported above may apply from time to time even when the pack is of minimum thickness, about 1–1⅛ inches.

ACKNOWLEDGMENTS

The authors wish to thank the management and staff of Job Brothers and Company, Southside, St. John's, for providing freezing facilities and for assistance in these experiments, and Mr E.E. Coldwell for his help in the work.

REFERENCES

CHARM, STANLEY. 1962. A method for experimentally evaluating heat transfer coefficients in freezers and thermal conductivity of frozen foods. *Food Technol.*, **17**: 93–96.

DYER, F.E., AND W.J. DYER. 1949. Changes in the palatability of cod fillets. *J. Fish. Res. Bd. Canada*, **7**: 449–460.

DYER, W.J. 1951. Protein denaturation in frozen and stored fish. *Food Res.*, **16**: 522–527.
1953. Main problems of fish protein denaturation. Proceedings of the Symposium on Cured and Frozen Fish Technology. *Swedish Inst. Food Preserv. Res. (Göteborg) Publ.* No. 100 (Chap. VII), 12 pp.

DYER, W.J., AND J.R. DINGLE. 1961. Fish proteins with special reference to freezing, pp. 275–327. *In* Georg Borgstrom [ed.] Fish as food, Vol. 1. Academic Press, New York.

DYER, W.J., DORIS I. FRASER, D.G. ELLIS, D.R. IDLER, W.A. MACCALLUM, AND E.J. LAISHLEY. 1962. Quality changes in stored refrozen cod fillets. *Supplement au Bulletin de l'Institut International du Froid*, Annexe 1962–1, pp. 515–524.

DYER, W.J., DORIS I. FRASER, D.G. ELLIS, AND W.A. MACCALLUM. 1957. Influence of intermittent short storage periods at 15°F, as encountered during refrigerator car transportation on the quality of frozen cod stored at 0°F. *J. Fish. Res. Bd. Canada*, **14**: 627–635.

GUTSCHMIDT, J. 1963. Organoleptic and physical methods to determine the texture of fish. *C.R. 11th Congr. Int. Froid*, Paper IV–33, 8 pp.

KONDRUP, M., AND H. BOLDT. 1960. The influence of the freezing rate upon the quality of frozen meat and poultry. *Supplement au Bulletin de l'Institut International du Froid*, Annexe 1960–3, pp. 309–330.

LEVY, F.L. 1958. Calculating the freezing time of fish in air-blast freezers. *J. Refrig.*, **1**(3): 55–58.

LONG, R.A.K. 1955. Some thermodynamic properties of fish and their effect on the rate of freezing. *J. Sci. Food Agric.*, **6**(10): 621–633.

LOWE, E., G.S. SMITH, AND O.H. SPAUGH. 1950. How to test your air-blast freezer. *Food Ind.*, **22**: 638.

MACCALLUM, W.A. 1955. Necessary equipment for the freezing of fish. *C.R. 9th Congr. Int. Froid*, 2, 4.32, 4096–4103.

MACCALLUM, W.A. AND D.G. ELLIS. 1964. Water-thawing of frozen cod blocks. *J. Fish. Res. Bd. Canada*, **21**(1): 115–131.

MACCALLUM, W.A., H.S. SHIEH, DOROTHY A. CHALKER, W.J. DYER, AND D.R. IDLER. 1964. Polyphosphate treatment of frozen cod. 2. Effect on drip, yield, lipid hydrolysis and protein extractability in twice-frozen Newfoundland summer trap and fall cod. *J. Fish. Res. Bd. Canada*, **21**(3): 539–548

MACFAYDEN, D.A. 1927. The investigation of drip and juice available for drip in frozen fish. *Biol. Bd. Canada, MS Rept. Experimental Stat.*, No. 24, 14 pp.

MACKAY, D.D., AND C.B. WELD. 1926. Structural changes of fish muscle during freezing. *Biol. Bd. Canada, MS Rept. Experimental Stat.*, No. 15, 19 pp.

MERRITT, J.H., AND J. TEMPLETON. 1963. Freezing of fish in vertical plate freezers — effect of loading procedure. *World Fishing*, September, 7 pages.

NAGAOKA, J., S. TAKAJI, AND S. HOHANI. 1955. Experiments on fish freezing in air-blast freezers. *Proc. 9th Int. Congr. Refrig.*, Vol. 2, Paper 4, 321.

NOTEVARP, O., AND E. HEEN. 1940. Über den Einfluss der Gefriergeschwindigkeit, der Lagertemperature und der Frische des Rohmaterials auf die Qualitat defrorener Fische. *Z. ges. Kälte-ind. Beih.*, **47**: 122–126.

PLANK, R. 1913. The freezing time of ice blocks. *Z. ges. Kalte-ind.*, **20**: 109–114.
1941. Contributions to the calculation and evaluation of the rate of freezing of foodstuffs. *Z. ges. Kälte-ind. Beih. Reihe*, **3**, H. 10, 1941.

SLAVIN, JOSEPH W. 1964. Freezing seafood — now and in the future. *Ashrae J.*, May 1964, pp. 43–48.

STILES, WALTER. 1922. The preservation of food by freezing with special reference to fish and meat: A study in general physiology. *Food Invest. Bd., London*, Special Report No. 7.

WATZINGER, A. 1951. Contact freezing of fish fillets between parallel plates. *C. R. 8th Congr. Int. Froid*, pp. 397–401.

WELD, C.B. 1927. Structural changes in fish during freezing and storage. *Biol. Bd. Canada, MS Rept. Experimental Stat.*, No. 12, 63 pp.

YOUNG, O.C. 1938. The quality of fresh, frozen and stored halibut as determined by a tasting panel. *Fish. Res. Bd. Canada, Prog. Rept., Pacific Coast Sta.*, No. 37, pp. 12–16.
1939. Further tasting panel tests on frozen and stored fish. *Ibid.*, No. 42, pp. 16–20.

YULE, P.A.A., AND G.C. EDDIE. 1953. A vertical plate freezer for whole fish. *Modern Refrigeration*, December, 1953.

Preliminary Trials of a Tag for Salmon and Lobsters[1]

By D. J. Scarratt and P. F. Elson

Fisheries Research Board of Canada
Biological Station, St. Andrews, N. B.

ABSTRACT

A description is given of a new design of toggle tag which can be easily embedded in the musculature of small marine animals. A brief account is included of preliminary trials on Atlantic salmon, cod, and lobsters.

INTRODUCTION

For some time one of us (P.F.E.) has been attempting to develop a tag which could be applied to young salmon (*Salmo salar*) 3–4 inches (1 inch = 2.54 cm) in length and be carried through to maturity. Previously reported systems (for a review see ICNAF Special Publication No. 4, 1963) did not seem to fulfil all requirements. Attention became focused on the system by which the parasitic crustacean, *Sphyrion lumpi*, is attached to its host, the redfish (Templeman and Squires, 1960). The female of this copepod has a hammer-shaped cephalothorax or "head" which becomes embedded in the flesh of the host, the rest of the body remaining outside. This head becomes encysted and may persist for many years after the main body of the parasite breaks off.

Description of Tag

An anchor was designed to approximate the profile of the head of *Sphyrion* by bending a small piece of wire to form three loops which provided an attachment point for a filament in the middle and gave a toggle effect to the anchor. In this way, sharp points which might irritate the wound were eliminated. One of the end loops was closed and the other left open so that it could be inserted in the hollow tip of a No. 20 hypodermic needle (Fig. 1).

Pull-out tests with freshly killed young herring indicated that, with the gauge and temper of wire used (0.013-inch stainless steel spring wire), an overall anchor length of 7–8 mm held well. With longer anchors of this material the arms sometimes bent at the centre loop and holding power was reduced (Fig. 2).

Polyethylene monofilament of 12 mil diameter (1 mil = 0.001 inch = 0.025 mm) having a breaking strength between 3 and 4 lb (1 lb = 0.45 kg) proved in tank tests to be a suitable material for attachment of anchor to label.

[1]Received for publication September 14, 1964.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

Labels were of paper laminated in polyethylene. Such labels float free of the fish's body, thus reducing abrasion of the skin.

Use on Salmon

The tag was attached by first threading the open end of the anchor into a No. 20 hypodermic needle which was then thrust into the musculature of the fish below the dorsal fin and between the main supporting bones of the fin so that on withdrawal of the needle the anchor was left on the far side of these bones (Fig. 2). Since it was found that scales carried in with the anchor delayed healing, a few scales were scraped from the insertion point before application. The tagging operation is fast and relatively simple.

In tank experiments, tags with 7-mm "sphyrion" anchors were carried satisfactorily by parr about 4 inches long for 4 months (Fig. 3) and by cod (*Gadus morhua*) of 5–6 pounds for the same period. With the latter species braided Terylene filaments were used satisfactorily, although healing in salmon parr with this filament was not as good as with the polyethylene.

In the autumn of 1960, 1000 tags of this type with single polyethylene filaments and labels of paper-polyethylene laminate were attached to hatchery parr which were then liberated in the Pollett River, New Brunswick. Some 2 dozen tags were recovered from merganser stomachs over the next 6 months. About as many more were seen on salmon smolts migrating seaward in the following June. In that month an additional 1000 tags were attached to hatchery smolts liberated in the same stream and 600 to smolts liberated in the Margaree River, Nova Scotia. Another 400 were attached to Margaree smolts in the spring of 1962. On the Margaree, Carlin tags were attached to over 1000 other salmon smolts as a control. To date (October 1964) there have been no adult returns from these field trials of the "sphyrion" tag and very few returns from the Carlin tags (Carlin, 1955) attached at the same time, although Carlin tags have already given about 1.5% returns from similar liberations in the Margaree River in 1963.

Anchors of this pattern have also been used by the Department of Fisheries of Canada, but using metal rather than plastic labels. These were attached to salmon and shad, *Alosa sapidissima*, that also carried monel-metal cattle ear-tags clipped to the caudal peduncle. Of 156 summer-tagged adult salmon, each carrying an ear-tag and a "sphyrion" tag, 21 were reported by late November; 18 of these carried the ear-tags and 14 carried "sphyrion" tags; 11 still carried both tags. Considerable lesion had developed around the ear-tags but there was little or none associated with the "sphyrion" tags. A shad carrying a "sphyrion" tag was recaptured one full year after the tag was applied.

Application to Lobsters (*Homarus americanus*)

Many devices have been used for tagging lobsters but with one exception, developed by Dr G.F.M. Smith, these are all lost when the animal moults

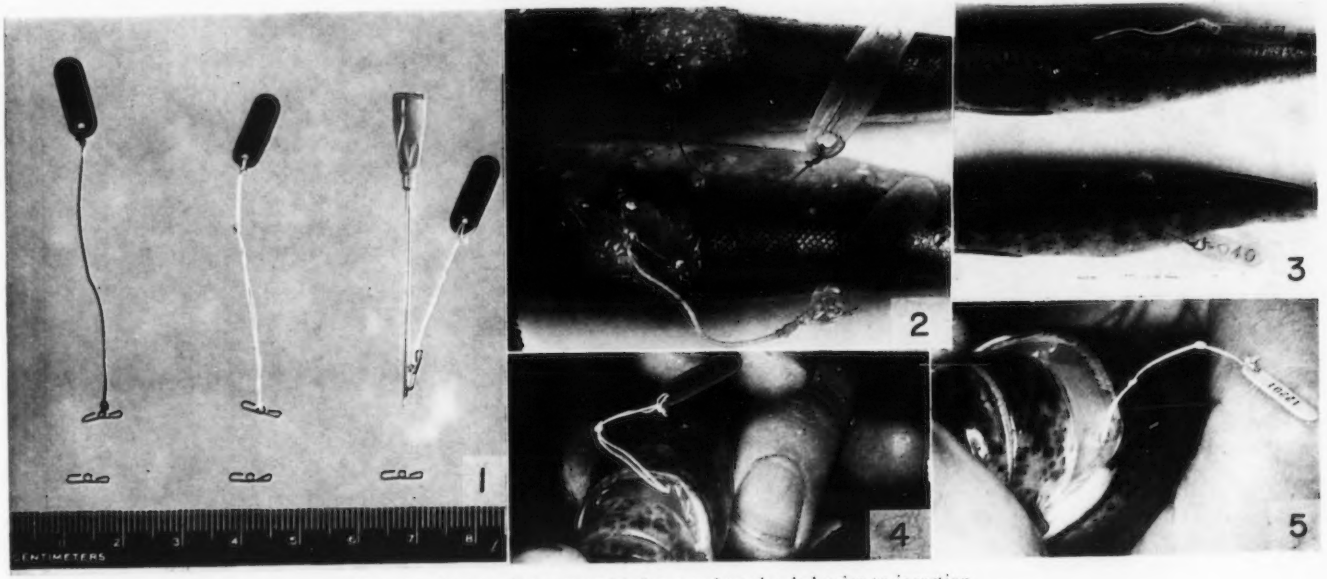


FIG. 1. Tag anchors, assembled tag and tag loaded prior to insertion.

FIG. 2. Dissections of the two salmon in Fig. 3. The small anchor promoted more rapid encystment.

FIG. 3. Two salmon parr 1 month after tagging with prototype "sphyrion" tags. Upper fish with a monofilament; lower fish with a filament of shirring elastic wound with nylon.

FIG. 4. Four-inch live lobster, 6 months and one moult after tagging.

FIG. 5. Seven-inch live lobster, 6 months and one moult after tagging.

(Leim, 1939). Dr Smith developed a celluloid dart tag which was inserted dorsally into the abdominal musculature of the lobster. Diagonal cuts in the celluloid acted as barbs to anchor the tag. In tank tests this tag caused some shell erosion and infection around the wound. Moreover, some of the tags worked into the flesh and were completely covered. Some 2000 lobsters were tagged in this manner and released in 1939–40 but returns were not as high (54%) as with cattle ear-type telson tags (59%) (Leim, 1940; M'Gonigle and Needler, 1941). Tags of this type have been used on spiny lobsters. (For a review of Crustacea tagging methods see Simpson, 1963.) Suture tags have been developed for use on crabs but these do not lend themselves to attachment through the delicate membrane between carapace and abdomen of the lobster.

With the thought that the "sphyrion" tag inserted through the membrane between carapace and abdomen and into the dorsal musculature would be retained by the lobster on moulting, in the manner of a suture tag, a small experiment was conducted. In January 1964, 14 lobsters ranging from 4 to 8 inches total length were tagged. The tags consisted of a "sphyrion" anchor, a double filament of polyethylene, and a small vinyl label.

Twelve of the 14 lobsters were placed in a large shallow tank, the bottom of which was covered with gravel and large rocks. They followed their usual practice of creating burrows under the rocks. No tags were lost through abrasion.

Of the 8 lobsters which have subsequently moulted, 7 retained the tag. One small lobster has retained the tag through two moults. Puncture wounds in most cases were clean and healed well (Fig. 4, 5). Growth increments were about average for lobsters held in captivity under similar temperature conditions indicating that there were no unduly deleterious effects. All lobsters retained complete mobility and did not show any signs of distress.

Additional experimental work is required to assess tag loss and tagging mortality.

REFERENCES

CARLIN, B. 1955. Tagging of salmon smolts in River Lagan. *Rept. Inst. Freshwater Res., Drottningholm*, No. 36, pp. 57–74.

ICNAF. 1963. North Atlantic Fish Marking Symposium, Woods Hole, Mass., 1961. *Intern. Comm. for the NW Atl. Fisheries, Spec. Publ.* No. 4, 370 pp.

LEIM, A. H. 1939. App. I, Rept. of the Atlantic Biological Station, St. Andrews, N.B., for 1938. *Annual Report of the Fisheries Research Board of Canada*, Ottawa, p. 21.
1940. App. I, Rept. of the Atlantic Biological Station, St. Andrews, N.B., for 1939. *Ibid.*, pp. 12–13.

M'GONIGLE, R. H., AND A. W. H. NEEDLER. 1941. App. I, Rept. of the Atlantic Biological Station, St. Andrews, N.B., for 1940. *Annual Report of the Fisheries Research Board of Canada*, Ottawa, pp. 13–14.

SIMPSON, A. C. 1963. Marking crabs and lobsters for mortality and growth studies. In North Atlantic Fish Marking Symposium, Woods Hole, Mass., May 1961. *ICNAF Special Publication* No. 4, pp. 188–193.

TEMPLEMAN, W., AND H. J. SQUIRES. 1960. Incidence and distribution of infestation by *Sphyrion lumpi* (Krøyer) on the redfish, *Sebastes marinus* (L.), of the western North Atlantic. *J. Fish. Res. Bd. Canada*, **17**(1): 9–31.

Lethal Levels of Mixed Copper–Zinc Solutions for Juvenile Salmon[1]

By J. B. Sprague and B. Ann Ramsay[2]

Fisheries Research Board of Canada
Biological Station, St. Andrews, N. B.

ABSTRACT

The toxicity of copper and zinc sulphates to juvenile Atlantic salmon (*Salmo salar* L.) was tested in very soft water at 17°C. The salts were tested separately and in mixtures. Incipient lethal levels were 32 μg/litre of copper alone or 420 μg/litre of zinc alone.

Concentrations were expressed in "toxic units" by taking them as proportions of incipient lethal levels. Compared this way, resistance-times were similar for the two metals. Experiments showed that the incipient lethal level for mixtures was attained when addition of toxic units contributed by each metal reached a total of 1.0. The lethal threshold was therefore governed by simple additive effect of the two toxicants. This result is useful for applying to pollution problems in the field.

In stronger mixtures totalling 2 and 5 toxic units, fish died faster than would be expected from their resistance to the metals separately. This type of potentiation in short-term tests seems to account for more-than-additive effects previously reported in the literature.

RÉSUMÉ

La toxicité des sulfates de cuivre et de zinc, mis séparément puis mélangés, a été déterminée dans une eau douce chez les saumoneaux de l'Atlantique au stade parr.

Les seuils des concentrations léthales sont 32 μg/litre de cuivre ou 420 μg/litre de zinc, à 17°C, à un pH de 7.0–7.4 et une dureté d'eau équivalent à 14 mg/litre de $CaCO_3$.

Les seuils des concentrations léthales ont été utilisés comme unité de concentration ("unité toxique"). Comparées sur cette échelle les durées médianes de résistance du poisson sont égales pour les deux sels.

Les expériences ont indiqué que le seuil de concentration léthale des mélanges est obtenu lorsque les contributions totales des deux métaux, en "unités toxiques" ont atteint 1.0. Cela indique que l'effet des deux métaux pour déterminer le seuil est précisément additif. Ce résultat est utile et peut s'appliquer aux problèmes des rivières polluées.

Dans les concentrations plus fortes des mélanges (2 et 5 unités toxiques) les saumoneaux sont morts plus vite qu'on s'y attendait en supposant que l'action toxique des deux métaux était additive.

INTRODUCTION

Copper and zinc often occur together as pollutants, as in a case of mining pollution in northern New Brunswick (Sprague *et al.*, 1964). In order to assess danger to Atlantic salmon, the major sport fish of that region, it is desirable to know the toxicity of the two metals acting together. Resistance of salmon to the metals singly has been described (Sprague, 1964a). However, that work did not show whether the incipient lethal level of mixtures was simply additive,

[1]Received for publication August 13, 1964.
[2]Present address (B.A.R.): Zoology Dept., University of Western Australia, Nedlands, Western Australia.

J. Fish. Res. Bd. Canada, 22(2), 1965.
Printed in Canada.

or different than would be predicted from the separate toxicities of the metals. The purpose of the present work is to demonstrate the threshold of joint lethal effects.

The general approach of "adding up" toxic effects of two or more pollutants has been extensively developed at the British Water Pollution Research Laboratory (Herbert and Shurben, 1964; Lloyd and Jordan, 1964). Instead of expressing concentrations in terms of conventional chemical units, they were expressed as proportions of their threshold or incipient lethal levels. The *incipient lethal level* (ILL) is considered to be that level of the lethal identity beyond which the organism can no longer survive for an indefinite period of time (Fry, 1947). The concept seems to have been first used in studies of pollution and fish by Bergström and Vallin (1937). They expressed strengths of pulp mill wastes in terms of a *giftenhet* or "toxic unit" based on the maximum level which allowed fish to survive for at least 5 days. They used the units for comparing toxicities of various components of pulp mill waste, but not for "adding up" to predict toxicity of mixtures. We have adopted previous terminology by assigning a value of 1.0 *toxic units* to the incipient lethal level of any toxicant. Thus a solution of a toxicant which is only half as strong as the ILL would have 0.5 toxic unit, and a solution twice as strong would have 2.0 toxic units.

This system has the advantage of measuring the strengths of different toxicants in terms of an equal effect on fish. By adding together toxic units contributed by different toxicants, we can interpret experiments with mixtures more easily, to see whether pairs of toxicants act together ("synergism"), have no interaction, or oppose each others action ("antagonism").

The system has already been applied to toxicity of copper–zinc mixtures for another species of salmonid, by Lloyd (1960, 1961) and Lloyd and Herbert (1962). They found that toxic units of zinc and copper were simply additive, and interchangeable for most conditions of the experiment.

MATERIALS AND METHODS

Bioassays were carried out in June 1963. Our procedures closely followed those previously reported (Sprague, 1964a), with minor changes recorded below.

Chemical procedures were similar to those in "Standard Methods" (APHA, 1960). They have been recorded in a manuscript (Sprague and Carson, MS, 1964) along with tests of accuracy and precision of metal analyses. All concentrations of metal are given in micrograms of metal (Cu or Zn) per litre of solution.

The water used in this work was taken from the same source as previously, but was considerably softer, with total hardness during acclimation and tests consistently being 14 mg/litre as $CaCO_3$. The reduction in total hardness probably resulted from a decrease in amount of calcium dissolved from a concrete pipeline (Sprague, 1964b). Water temperature during acclimation and testing was $17.0 \pm 0.5°C$, and pH was from 7.0 to 7.4, generally about 7.3.

The laboratory water contains 3 μg/litre of zinc, as judged by analyses over several years, and 2 μg/litre of copper (Sprague and Carson, MS, 1964).

Yearling salmon were obtained from the Department of Fisheries of Canada hatchery at Saint John, N.B., where they had been reared in soft water. They were held at our laboratory, with no mortality, for 21 days before testing. During the last 10 days of this, fish were held at the exact experimental conditions of temperature and pH, and during the first 11 days conditions had approximated those of the experiment but were not so closely controlled. Length and weight of fish were measured when their death was detected, or at the end of a bioassay. The average fork length was 9.2 cm with a range of 7.2–10.9.

All bioassays were of the continuous-flow type, with 300 ml/min of fresh solution passing into the 27-litre experimental tanks. All components of the apparatus which contacted experimental water were glass, Fiberglas, Plexiglas, Tygon or other plastics.

The concentration of metals in the experimental water was determined at least once a day, and determinations for a given bioassay were averaged and used as the experimental condition. Deviations of individual copper determinations from the mean value of each experiment averaged only 5 μg/litre, and none was greater than 20 μg/litre. Deviations of individual zinc determinations averaged only 5% of the mean value for the experiment, and did not exceed 25%. The largest deviations were not critical in the particular bioassays involved. Some of this apparent scatter would result from analytical error. Tests have shown that averages of several replicate analyses done in our laboratory are accurate, but single measurements of copper have 95% confidence limits of ±9 μg/litre, while single zinc measurements have confidence limits of ±6%, which would be ±25 μg/litre in the region of the ILL for zinc (Sprague and Carson, MS, 1964). Concentrations of zinc measured in the test tanks agreed with intended concentrations, averaging 104% of intended levels. Measured copper concentrations averaged 94% of intended levels, probably because of sorption from these very weak solutions.

Eight fish were used in each bioassay to measure the time to 50% mortality, or LT50. The order of starting tests in the six experimental tanks, and assignment of fish to tanks, were randomized as far as possible. Times of death of individual fish were considered to be half-way between adjacent times of inspection, which increased more or less logarithmically. Tests were terminated at 1 week (168 hr). Results were analyzed by the methods of Litchfield (1949), which include appropriate modifications for estimating LT50s from truncated distributions, which result from incomplete mortality in groups of test animals.

RESULTS

Details of lethal tests are given in Table I, and LT50s for the metals acting singly are shown in Fig. 1. A word of explanation is required for the manner of plotting zinc concentrations. Since we know that copper is approximately 12.5 times as toxic as zinc, and that lethal effects of the two

metals are at least additive (Sprague, 1964a) we must make some allowance for the small amounts of copper naturally present in the water used for zinc experiments. The 2 μg/litre of copper in laboratory water must be considered, as a first approximation, to be equal in effect to 25 μg/litre of zinc. This value of 25 has been added to the measured concentrations of zinc for the purpose of constructing Fig. 1. The small amount of zinc present in laboratory water is equivalent to only 0.2 μg/litre of copper and may be neglected.

The use of logarithms in Fig. 1, for both concentration of metal and exposure time, allows the points to be reasonably represented by straight lines. For copper, it is evident that there is a sharp break in the relation at the incipient lethal level. The ILL must be closer to 34 μg/litre, at which there was exactly 50% mortality, than 28 μg/litre, at which there was no mortality. The ILL is estimated as 32 μg/litre of copper.

For zinc, the experiment at 435 μg/litre of zinc (410 μg/litre Zn + the copper equivalent of 25 μg/litre Zn) was obviously very close to the ILL. The

TABLE I. Details of experiments on mortality of young salmon exposed to copper and zinc solutions. Tests were done in June 1963 in water of 14 mg/litre total hardness, 17°C, and pH 7.0–7.4. Toxic units were calculated after the incipient lethal levels of individual metals had been estimated. Complete mortality occurred in each test unless indicated otherwise.

Metal (μg/litre)				
Copper	Zinc	Metal (toxic units)	LT50 (*hr*) (and 95% confidence limits)	Comments
28	3	0.88	0% dead in 168 hr	
34	3	1.07	27.6 (18.9, 40.3)	50% survival at 168 hr[a]
49	3	1.5	17.5 (13.6, 22.6)	
220	3	6.9	3.6 (2.7, 4.8)	
2	300	0.78	12.5% dead in 168 hr	
2	410	1.04	58.0 (26.4, 128)	50% survival at 168 hr[a]
2	650	1.6	15.6 (14.1, 17.3)	
2	1060	2.6	9.4 (6.6, 13.3)	
2	4190	10.0	2.6 (2.1, 3.2)	
14	200	0.91	0% dead in 168 hr	
15	230	1.02	36.0 (19.7, 65.9)	50% survival at 168 hr[a]
24	460	1.8	4.3 (3.3, 5.6)	
65	1210	4.9	2.3 (2.0, 2.7)	
2	3	0.07	0% dead in 168 hr	Control experiment

[a]The LT50 and confidence limits in this experiment were estimated by the appropriate method for truncated distributions (Litchfield, 1949).

first three fish to die indicated an LT50 of about 40 hr, but the fourth fish, which would make 50% mortality, did not die until considerably later. Apparently it was on the borderline of survival, since no further mortality occurred in the group. The result of this was an LT50 longer than any others recorded in these or previous tests with salmon (Sprague, 1964a). Usually 50% mortality occurred within about 40 hr or not at all. The vertical line in Fig. 1 indicating the ILL has been drawn at 420 μg/litre of zinc, very close to the "borderline" test at 435 μg/litre.

Also indicated in Fig. 1 are results from the previous set of tests in slightly harder water of 20 mg/litre total hardness compared to the present 14 mg/litre. The decrease in resistance in the softer water is expected (Lloyd and Herbert, 1962). The difference between the two sets of results is very regular for zinc, and there is a similar decrease in ILL for copper, although the line fitting resistance-times has a different slope.

Having determined the ILLs, concentrations of copper or zinc may be expressed as toxic units by taking them as proportions of the ILLs. Strength of mixtures may be expressed by adding together toxic units contributed by each metal. Results have been plotted this way in Fig. 2. The lines for copper

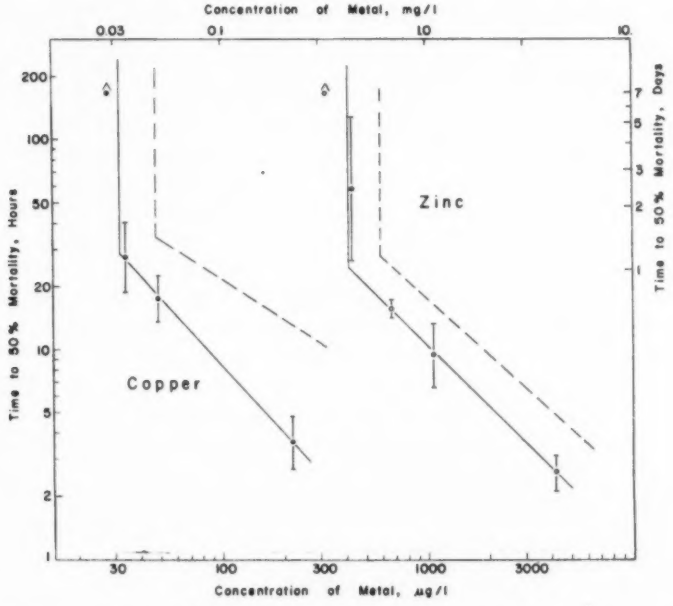


FIG. 1. Median mortality-times of young salmon exposed to solutions of copper and zinc. Vertical bars indicate 95% confidence limits of the LT50s. The fitted straight lines break and run parallel to the time-axis at the *incipient lethal levels*. The broken lines represent results obtained previously (Sprague, 1964a) in somewhat harder water.

and zinc are very close. A single curve could be used to fit the sets of points for both copper and zinc, yet there would still be an abrupt break at the ILL.

Survival time in lethal mixtures is much reduced, indicating that the metals potentiate each other's lethal action in the restricted sense of rapidity of death of fish. However the ILL for mixtures seems to be simply additive. Certainly there is little or no potentiation with regard to the ILL, since no mortality occurred at 0.91 toxic unit. In addition, we were fortunate to have one test at almost exactly the threshold of lethal effect, 1.02 toxic units, in which mortality ceased at 50%, with a prolonged LT50 as had happened with the zinc test at 1.04 toxic units. The incipient lethal level for mixtures must be 1.0 or very close to it.

DISCUSSION

Incipient lethal levels of 32 μg/litre of copper and 420 μg/litre of zinc are reasonable for a water hardness of 14 mg/litre. The decreased resistance compared with previous tests in water of 20 mg/litre hardness (Fig. 1) agrees with the magnitude of change with hardness as determined by others (Lloyd and Herbert, 1962; Tarzwell and Henderson, 1960).

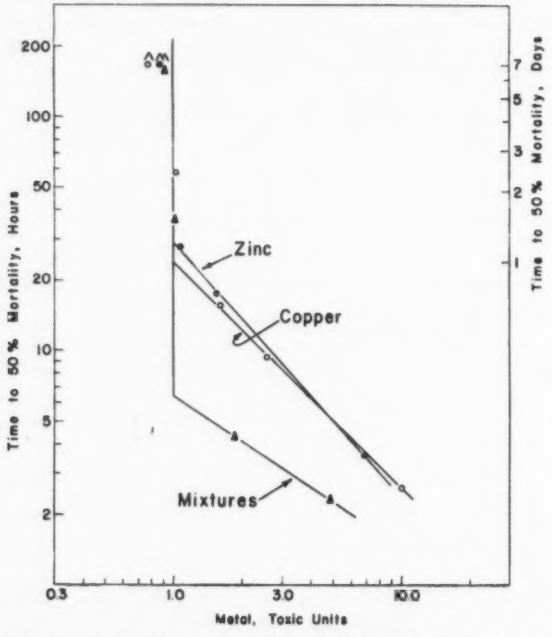


FIG. 2. Comparison of median mortality-times of young salmon exposed to solutions of copper, zinc, and mixtures. Toxic units for each metal are calculated as fractions or multiples of its incipient lethal level. Strength of mixtures is expressed by adding together the individual toxic units for zinc and copper.

As was found previously, salmon parr are slightly less resistant to these metals than are rainbow trout: for 14 mg/litre total hardness, ILLs for copper and zinc are 32 μg/litre and 420 μg/litre compared to 37 μg/litre and 560 μg/litre for rainbow trout (Lloyd and Herbert, 1962). A slightly greater difference between the resistance of the two species to zinc was found by Herbert and Wakeford (1964), who worked with salmon in the smolt stage, and compared concentrations causing 50% mortality in 48 hr.

Resistance-times of salmon for the metals acting singly are almost identical when concentrations are plotted in toxic units (Fig. 2). Previous work showed zinc was more rapidly lethal (Sprague, 1964a) and no explanation of the difference is apparent. The present findings are similar to those of Lloyd (1961).

Lethal concentrations of mixtures act two or three times as fast as the metals singly, a somewhat greater potentiation than was found in the previous tests with salmon. Probably the more extreme effect results from the softer water. Lloyd (1961) found potentiation only in soft water and concentrations greater than 7.0 toxic units. Such potentiation in short-term lethal tests seems to be the source of common reports of this phenomenon in the literature, such as the review by Doudoroff and Katz (1953).

More useful in practical work with pollution problems is the simple additive action in determining the incipient lethal level of mixtures. A mixture of 0.91 toxic unit did not cause any mortality. The surprising exactness of addition is shown by the test with a mixture of 1.02 toxic units, which killed just half of the fish. This agrees with the additive effect of copper and zinc in determining the lethal threshold for rainbow trout (Lloyd, 1961). Other common pollutants may apparently be "added up" in a similar way (Lloyd and Jordan, 1964) but Herbert and Shurben (1964) point out that the method is best used only for incipient lethal levels, since it does not always give a good prediction of survival times in higher concentrations.

The value of this tool for assessing danger of pollution to fish can scarcely be overestimated. There has been no simple way of expressing, or working with the effects of, two or more pollutants occurring together. In cases where the method is shown to be applicable, it is a most profitable means of translating from chemical analyses to effects on fish, and vice versa, as has been shown in British work on polluted streams (Lloyd and Jordan, 1964). Certainly the system will be useful for quantifying and explaining toxicity of base metal mining pollution in New Brunswick, since copper and zinc seem to be the only major contaminants (Sprague *et al.*, 1964).

ACKNOWLEDGMENTS

Chemical analyses were carried out by W. Victor Carson, and Michael G. Dionne inspected fish mortality at night. Young salmon were obtained from the Department of Fisheries of Canada Fish Culture Station in Saint John, N.B., supervised by Mr A.J. Baxter.

REFERENCES

APHA. 1960. Standard methods for the examination of water and wastewater. American Public Health Assoc., Inc., New York, 11 ed., 626 pp.

BERGSTRÖM, H., AND S. VALLIN. 1937. Vattenförorening genom avloppsvattnet från sulfatcellulosafabriker. Kungl. Lantbruksstyrelsen. *Medd. Statens undersöknings- och försöksanstal för sötvattensfisket (Stockholm)*, No. 13, 19 pp.

DOUDOROFF, P., AND M. KATZ. 1953. Critical review of literature on the toxicity of industrial wastes and their components to fish. II. The metals, as salts. *Sewage Ind. Wastes*, **25**: 802–839.

FRY, F. E. J. 1947. Effects of the environment on animal activity. *Univ. Toronto Stud., Biol. Ser.*, No. 55; *Pub. Ontario Fish. Res. Lab.*, No. 68, 62 pp.

HERBERT, D. W. M., AND D. S. SHURBEN. 1964. The toxicity to fish of mixtures of poisons. I. Salts of ammonia and zinc. *Ann. Appl. Biol.*, **53**: 33–41.

HERBERT, D. W. M., AND A. C. WAKEFORD. 1964. The susceptibility of salmonid fish to poisons under estuarine conditions. I. Zinc sulphate. *Intern. J. Air Water Pollution*, **8**: 251–256.

LITCHFIELD, J. T., JR. 1949. A method for rapid graphic solution of time-per cent effect curves. *J. Pharmacol. Exp. Therap.*, **97**: 399–408.

LLOYD, R. 1960. The toxicity of zinc sulphate to rainbow trout. *Ann. Appl. Biol.*, **48**(1): 84–94.

1961. The toxicity of mixtures of zinc and copper sulphates to rainbow trout (*Salmo gairdnerii* Richardson). *Ibid.*, **49**: 535–538.

LLOYD, R., AND D. W. M. HERBERT. 1962. The effect of the environment on the toxicity of poisons to fish. *J. Inst. Public Health Eng.*, July, pp. 132–145.

LLOYD, R., AND DOROTHY H. M. JORDAN. 1964. Predicted and observed toxicities of several sewage effluents to rainbow trout: A further study. *J. Proc. Inst. Sewage Purification*, Part 2, pp. 3–6.

SPRAGUE, J.B. 1964a. Lethal concentrations of copper and zinc for young Atlantic salmon. *J. Fish. Res. Bd. Canada*, **21**(1): 17–26.

1964b. Highly alkaline water caused by asbestos-cement pipeline. *Prog. Fish-Culturist*, **26**(3): 111–114.

SPRAGUE, J.B., AND W.V. CARSON. MS, 1964. Chemical conditions in the Northwest Miramichi River during 1963. *Fish. Res. Bd. Canada, MS Rept. (Oceanogr. and Limnol.)*, No. 180, 62 pp.

SPRAGUE, J. B., P. F. ELSON, AND R. L. SAUNDERS. 1964. Sublethal copper-zinc pollution in a salmon river — a field and laboratory study. Presented at 2nd Int. Conf. on Water Pollution Research, Tokyo, August 1964.

TARZWELL, C. M., AND C. HENDERSON. 1960. Toxicity of less common metals to fishes. *Industrial Wastes*, **5**: 12.

Migrations of Harp Seals *Pagophilus groenlandicus* (Erxleben) in the Northwest Atlantic[1]

By D. E. Sergeant

Fisheries Research Board of Canada
Arctic Biological Station, Ste. Anne de Bellevue, Que.

ABSTRACT

Some 1300 harp seal pups were marked with four types of tags over 5 years from commercial sealing ships at the breeding patches off eastern Canada. Recovery rates from individual taggings ranged up to 20%. The greatest age at recovery was 4 years, 10 months. The recoveries and observational evidence show that the young seals at 4–6 weeks move out to the ice edge, drift passively with the prevailing current, and at 8–10 weeks begin to migrate northward, independently of and somewhat later than the herds of older animals. Tag recoveries in summer come from West Greenland and eastern Baffin Island. The southward migration begins in late September at high latitudes and reaches the Strait of Belle Isle by late December. Many immatures remain in arctic waters much later than the main herds, but the majority have moved south to join them in the breeding areas by April, when moulting takes place. Harp seals born in the Gulf of St. Lawrence and on the ice east of Belle Isle separate to their home areas to moult as immatures, although they mix in their summer range and on the southward migration. Probably, breeding and moulting adults remain distinct also. In the Gulf of St. Lawrence, most moulting takes place in the water, but east of Belle Isle, on ice. Moulting groups east of Belle Isle are composed at first of adult males and immatures, and are joined in the later part of April by the adult females which have given birth.

CONTENTS

	Page
Abstract	433
Previous Work and Scope of this Study	433
Material and Methods	435
First Movements of Young Seals	437
Summering of Young and Immatures	442
Southward Migration	445
Wintering	448
Breeding	448
Moulting	453
Summary	461
Acknowledgments	462
References	463

PREVIOUS WORK AND SCOPE OF THIS STUDY

Migrations of the western stock of harp seals have not been considered in detail before. Allen (1880) gives a brief account, as does Fisher (MS, 1954).

[1]Received for publication November 17, 1964.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

Robinson (1897) and Chafe (1923) compiled observations evidently given them by Newfoundland and Scottish sealing captains. Rasmussen (1957) and also Surkov (1960) give condensed accounts of migrations of the central or West Ice stock of harp seals, and Chapsky (1961) gives a detailed account of the annual migration pattern of the eastern or White Sea herd.

In this study all aspects of the annual cycle of the western harp seals will be considered in so far as they relate to the animals' movements. Physiological aspects of reproduction and moult, and details of feeding, however, are not considered here.

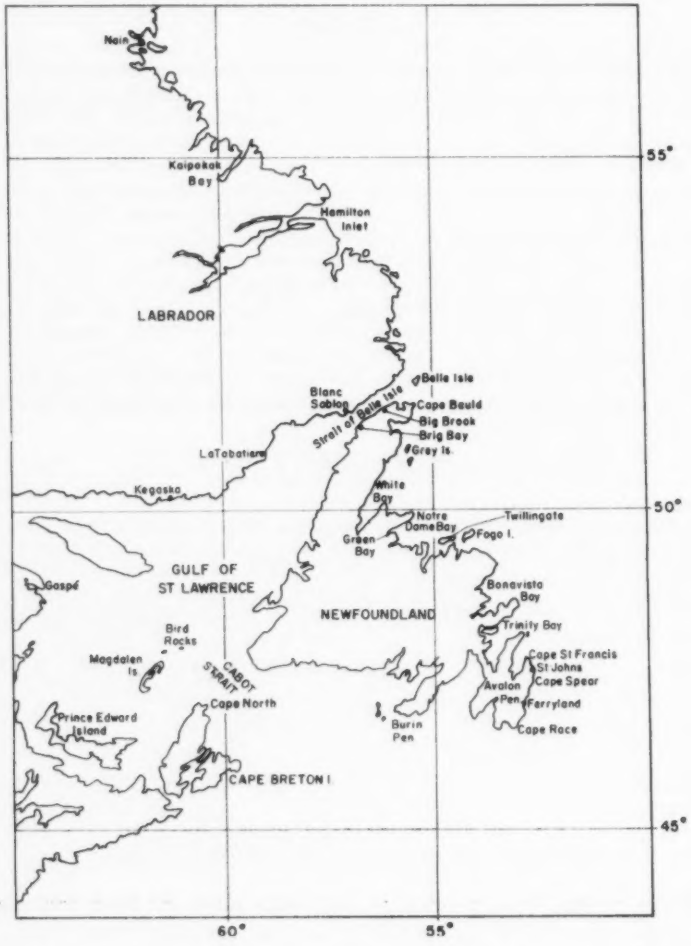


FIG. 1. Map showing place names mentioned in the text. (See also Fig. 5 and 6.)

For brevity, the sealers' names are used for the two main regions of ice inhabited by the seals. *Gulf* means the Gulf of St. Lawrence; *Front*, the ice east of northeast Newfoundland and southern Labrador. These regions are believed to be inhabited by two distinct stocks of harp seals, as discussed below.

The maps (Fig. 1, 5, and 6) show localities mentioned in the text.

Snow and ice terminology is that used by Armstrong and Roberts (1956, 1958), with the exception that the Newfoundlanders' term "slob" ice is preferred to "sludge" ice since the latter term is easily confused with "slush" which has quite a different connotation in the same glossary. (Sludge or slob is ice in process of formation from sea water in the series, frazil ice – sludge ice – pancake ice; slush results from snow falling on water.)

MATERIAL AND METHODS

Marking

Approximately 1300 newborn "whitecoat" harp seal pups were tagged at the breeding patches in early March of the years 1950–54 from commercial sealing ships. The distribution of tagging by year and area is shown in Table I. Note that twice as many seals were tagged on the Front as in the Gulf.

It is known that a percentage of the tags was retaken by ships' crews within a few days and not reported because this taking was discouraged, so that the number of seals effectively tagged was somewhat less, perhaps about 1000.

Distribution of tag types is shown in Table II. The majority (1077) of tags were monel metal disc tags bearing the legend "Canada Fisheries" and a serial number (Fig. 2). To the upper disc were soldered two nickel pins, which pierced the sides of the tail. A second disc, pierced to receive the pins, was placed on the under side of the tail. The pins were bent round with pliers to secure the tag loosely, allowing for some tail growth. These tags stayed on up to 4 years. Overall recaptures were only 76 out of 1077 (7.0%), but recaptures for individual tagging years reached 37 out of 304 (12.2%) and for

TABLE I. Marking by year and area.

Year	Gulf of St. Lawrence	East of Newfoundland
1950	125	–
1951	–	178
1952	203	371
1953	–	304
1954	116	–
Totals:	444	853
	1297	

TABLE II. Marking and recaptures by tag type.

Tag type	Year	Marked	Recaptured
Monel disc	1950	101	3
	1951	148	2
	1952	408	25
	1953	304	37
	1954	116	9
Cod belly	1952	94	2
Bachelor button	1952	72	4
Cattle ear	1950	24	1
	1951	30	–
Total:		1297	83

individual experiments 20 out of 98 (20.4%). Some bimetallic corrosion at the point of contact of discs and pins could probably be reduced by using discs and pins of the same metal. Corrosion of the solder is unimportant since the pins are headed and cannot slip out. The great virtue of these tags is the speed and ease with which they can be attached.

Other tags used were a cattle ear tag of monel metal attached to the hind flipper, which gave one recovery out of 54 tags; a cod belly tag of cellulose acetate pierced at one end and attached by wire round a digit of the hind

FIG. 2. A whitecoat tagged in the tail with a disc tag.

flipper, which gave two recoveries out of 94 tags; and a circular "bachelor button" tag, one-half of monel and the other of cellulose acetate, the two halves of which were pressed together with special pliers round the web of the hind flippers after a circular piece of the web had been cut out with a leather punch. The last-named method gave four recoveries out of 72 tags.

In five cases of double tagging, two bachelor button tags fell off leaving the monel tail tags, two stayed on with them, and one cod belly tag stayed on with a monel tag. There does not seem to have been any advantage of the particular types of fore- or hind-flipper tags used over the tail tag. It is known from recent marking of grey seals (*Halichoerus grypus*) in Great Britain that wires or pins may be worked out of the sides of the tail by the drag which the tags set up. Norwegian investigators have used a single yellow and black plastic tag attached by wires pierced through the sides of the tail; Rasmussen and Öritsland (1964) have recently reported results. Such a tag is more conspicuous, but slower to attach, than a double metal tag with soldered pins. Some of our metal tags were painted red and were conspicuous for a short period.

The most unusual recapture came from a codfish (*Gadus morhua* L.) taken in Trinity Bay, eastern Newfoundland, in July 1955, 2 years and 3 months after tagging. Harp seals are not usually present at this time and it is surmised that the seal was killed or died as a pup and the tail with tag eaten by the cod. The disc still showed some red paint and little sign of wear.

Observations

Observations of living harp seals were made by the author from commercial sealing ships in cruises of 6–8 weeks duration in March–April of 1952–54; and from planes in the course of aerial photographic surveys of numbers of breeding seals in March of 1955, 1959, 1960, and 1964, and of moulting seals in April–May of 1961, and in April 1962 and 1963. Dr H. D. Fisher contributed observations made by him during similar cruises in 1949 and 1953, and on aerial surveys in 1950 and 1951. Dr A. W. Mansfield contributed observations from a tagging program in the Gulf carried out from a helicopter in March 1964.

Sampling

Sampling of jaws and subsequent determination of the age composition of harp seals were carried out at various times and places principally to study mortality rates and population dynamics. The samples show the age–sex composition of the seals at different seasons. Methods of age determination are discussed by Fisher (MS, 1954).

First Movements of Young Seals

Recaptures of tagged seals by area, season, and age are analysed in Table III.

TABLE III. Recaptures by area, season, and age. One tag, recovered in a cod stomach, is omitted.

Area	Year of life					
	First	Second	Third	Fourth	Fifth	Total
Icefields, Gulf of St. Lawrence	10	–	1	–	–	11
Icefields, east of Newfoundland	33	5	3	1	1	43
Greenland, summer and fall	14	7	–	–	1	22
Baffin Island, summer and fall	–	2	–	–	–	2
Labrador and Newfoundland, fall migration	2	1	1	–	–	4
Totals:	59	15	5	1	2	82

Recaptures of young seals taken by sealing ships and landsmen around eastern Canada in the first 3 months after birth (and tagging) are shown in Fig. 3. In order to lessen killing of newly-tagged animals no reward was paid for tags taken from young seals on shipboard so that recoveries from this source may be incomplete.

Aerial observations in Notre Dame Bay in late April 1961 showed a concentration of "beaters" — young, fully-moulted seals — at the border of ice and open water. In mid April 1952 it was noted from a ship jammed in the ice off the Grey Islands in White Bay that single beaters were on the move over the ice eastward, i.e. towards open water. They rested up by day but tracks showed their movement, presumably by night. In 1953, beaters taken from a sealing ship were found to be feeding on large quantities of euphausiids *Thysanoessa raschi* (M. Sars) from April 5 onward. Presumably then, this first movement of the young at an age of 4–6 weeks after birth serves to take them from the ice where they were born, which may be "tight" (i.e. without open water leads) and is probably less productive of food, to the ice edge where food is more abundant.

Subsequent movement is a drift of the young seals on the ice or in the water with the prevailing wind and current. This together with the melt and retreat of the ice in April will tend to bring the animals shoreward. In the Gulf of St. Lawrence the young are born in the general vicinity of the Magdalen Islands and Prince Edward Island. The drift of ice out of the Gulf tends to take the young east around Cape Breton Island, as shown by the majority of recoveries (Fig. 3). East of Newfoundland the breeding seals may be situated initially anywhere between outer Hamilton Inlet, Labrador, and Funk Island, Newfoundland, in one or two main groups. A current sets intermittently with a net southward flow into the Strait of Belle Isle and usually takes some breeding seals with it, but the main Labrador Current sets close along the

eastern coast of Newfoundland. Recoveries again show this (Fig. 3). The Labrador Current splits into two at the latitude of St. John's, Newfoundland, the outer branch following around the eastern edge of the Grand Bank, the inner branch continuing around Cape Race. Some young harp seals could be carried in the outer branch, and a young harp was reported seen on floating ice at 47°48′N, 50°00′ W on May 7, 1953, from a fishing trawler with a second taken from another ship on the previous day, presumably nearby.

The young taken in the bays of eastern Newfoundland in April and May had evidently not yet begun their northward movement. The latest date of recovery of a tagged seal was in Trinity Bay on May 21. This would seem to place the beginning of the northward movement mainly in the first half of May. Dr H. D. Fisher noted a northward movement of scattered young off southern Labrador as early as April 26, 1953, the seals swimming in open water. On May 1 other young which had evidently not yet begun to migrate northward were seen on ice further south. It is noteworthy that all the beaters

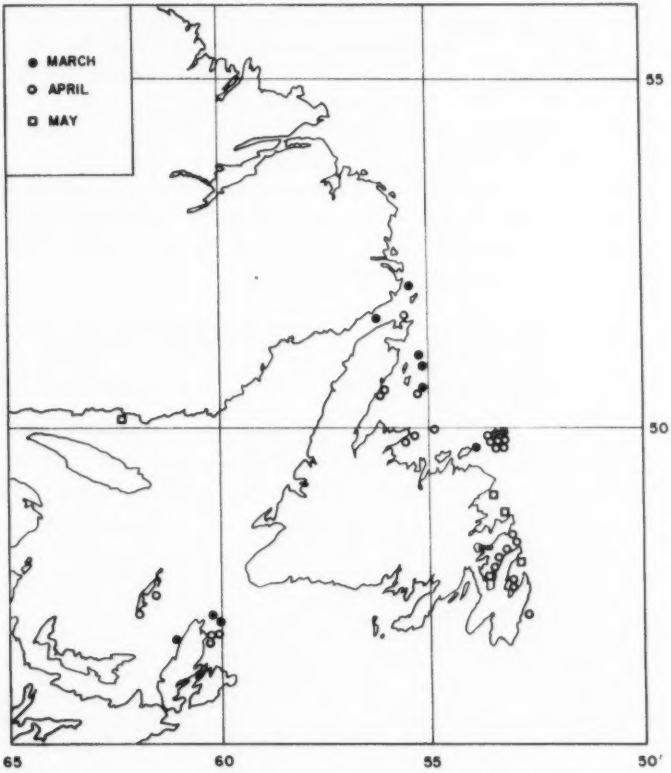


FIG. 3. Recaptures of tagged young harp seals in the first 3 months after birth and tagging.

seen by Fisher were swimming singly; the animals do not form schools at this stage.

Dr E. H. Grainger travelling on C.G.S. *Baffin* reported 40–50 seals, the closer ones identified as harp seals, along the outer border of the pack ice of the Labrador current between 52° and 54°N and 55° to 56°W on May 25, 1963. Some animals at least were young ones.

The single tag recovery from the north shore of the Gulf of St. Lawrence in May (Fig. 3), with exact date unknown, perhaps came after the individual had begun its northward migration.

The spring fishery for harp seals on the north shore is usually a small one, since as stated by Huntsman *et al.* (1954) the seals do not strike the coast till they reach the Strait of Belle Isle. The catch is largely on the north shore, and not on the Newfoundland side, that is, the migration proceeds against the prevailing current (for the oceanography, see Hunstman *et al.*, 1954). Statistics of the 1962 catch on the north shore (Table IV) show more young harps taken in June than in May, but more adult and immature harps taken in May than in June. Moreover, an age sample was obtained from the catch taken at Blanc Sablon in June 1957 and showed almost exclusively young animals (Fig. 4, upper). This information shows that on the average the migration of young through the Strait of Belle Isle follows that of the older animals, and is independent of it Again from the respective dates of departure of the young and older animals east of Newfoundland, the same must be true.

In summary, the young show two successive active movements separated by a passive stage. At 4–6 weeks they move over the ice from the site of birth towards open water, then drift passively with the current. At 8–10 weeks, they show an active northward movement.

TABLE IV. Catches of seals in Lower Saguenay County, from Kegaska to Blanc Sablon, Quebec, in the first half of 1962. Data courtesy Quebec Bureau of Statistics.

Month	Young harps	Immatures	Old harps	Unclassified	Total
Jan.		2,923	2,927	1,205	7,055
Feb.					
Mar.	4,175[a]				4,175
Apr.	885 459[b]	3	1		1,348
May	248	280	248		776
June	401	137	40		578
Totals:	6,168	3,343	3,216	1,205	13,932

[a]Loose-haired.
[b]"Young seals."

In the movement of young away from the breeding ice, hunger may be the stimulus, and open water and food the goal, of the appetitive behaviour. The orienting mechanism is unknown; much of the movement appears to be nocturnal.

Fisher's observations suggest that the subsequent northward movement may be initiated by disappearance of drift ice. As to possible mechanisms of orientation, the northward movement both east of Newfoundland and in the Strait of Belle Isle proceeds against a prevailing southward-flowing current. Possibly, celestial clues may be used. However Dr H. D. Fisher informs me also that he has seen schools of adult and immature seals in late April off the Labrador coast swimming northwards on a cloudy night. This was observed from a sealing ship, and other ships in the area reported the same direction of movement. The seals maintained their direction under loose ice fields. Seals in a circular aquarium swim round and round, so that experimental study of their orientation will require ingenuity.

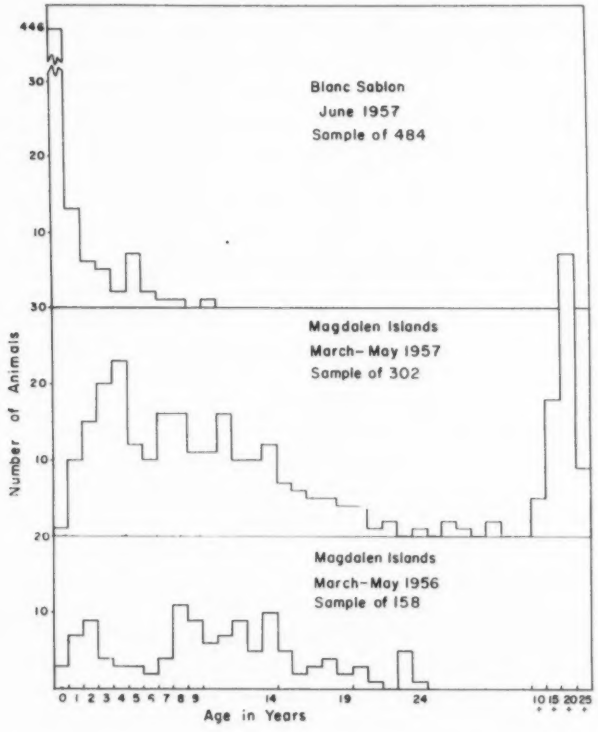


FIG. 4. Various age samples of harp seals from the Gulf of St. Lawrence.

SUMMERING OF YOUNG AND IMMATURES

Recaptures of marked young and older seals during the rest of the year (other than March to May) are shown in Fig. 5. It must be remembered that the hydrographic summer is 2–3 months later than the calendar summer.

There was a gap of nearly 4 weeks before the first marked young were recaptured in their summer range in West Greenland, a first-year animal being taken on June 17 at Narssalik, 61°38′N. Three out of four June recaptures were from this area of southernmost West Greenland, and all refer to first-year animals.

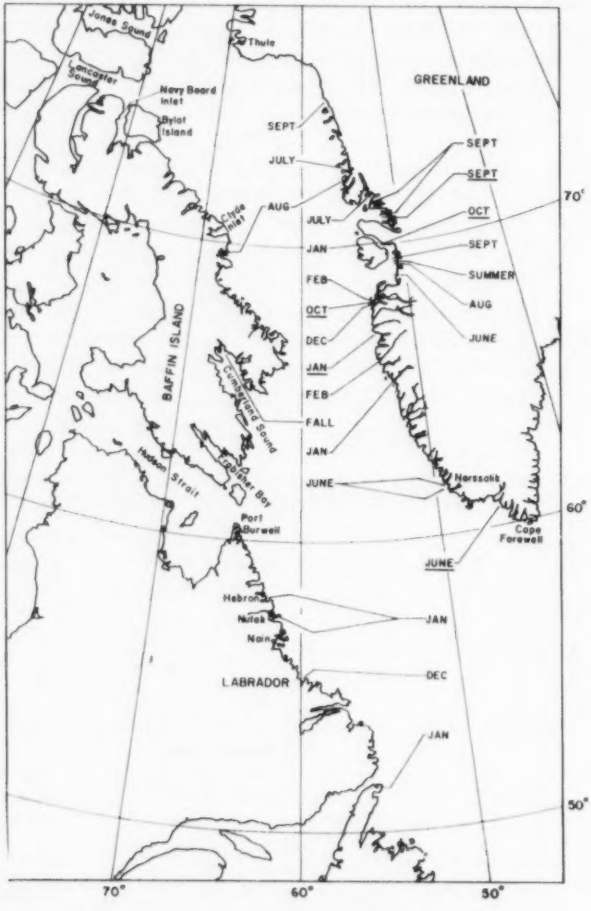


FIG. 5. Recaptures of young harp seals in all months other than March to May and at all ages. Underlines indicate seals tagged in the Gulf; all other seals were tagged on the Front.

Sixteen other Greenland recaptures ranged from 65° northwards to 74°N, and extended in time from late June to mid February, with recaptures in all intervening months except November. There were also two late summer recaptures from Baffin Island, at Clyde Inlet and Cumberland Sound.

Five Greenland recaptures were of animals marked in the Gulf, the remaining 24 summer or early winter recaptures being of animals marked on the Front. There is no apparent difference in range in Greenland between recaptures of Gulf- and Front-marked animals, and one supposes that a complete mixture takes place over the summering range.

The greater percentage of recaptures from Greenland waters than from the Canadian eastern arctic reflects the much greater kill of harp seals on the Greenland coast. Few are taken by Eskimos in the eastern Canadian arctic except on the southward migration at Port Burwell, Ungava. It is known, however, that harp seals enter Lancaster Sound and Jones Sound in large numbers in late summer, while they are common in Cumberland Sound, Frobisher Bay, and Hudson Strait, a few penetrating into northwestern and southeastern Hudson Bay. Probably the number of harp seals is much less on the Canadian than on the Greenland side of Baffin Bay and Davis Strait in early summer because there is much more ice on the Canadian side, but in late summer the difference may be less.

The northern limit of summering is the Thule district of northwest Greenland, the southern limit northern Labrador where harp seals remain in some summers.

Catch statistics for 1949–51 from Greenland have been analysed by Rosendahl (1961). The part of his chart which refers to West Greenland is shown as Fig. 6. The temporal and spatial variations in catch show that there are (1) a spring peak of harp seals taken in southwest Greenland from May to July; (2) two peaks in midwest Greenland, one in June and the second from September to January; and (3) a single, late-summer abundance of harp seals in northwest Greenland. The end of the first peak in midwest Greenland is said by Jensen (1928) to be due to the seals moving offshore when the capelin (*Mallotus villosus* Fabricius) cease spawning and become dispersed again, but is perhaps more likely due to the seals moving further to the north. Age samples from different settlements are being obtained by the Greenland Department of the Danish Government and analysed by the writer for a further study of age composition.

The catch statistics from Greenland also show that some seals are captured through March and April. If these are in fact harp seals, and we have no reason to doubt the statistics on this score, then we may suppose that some immatures — it cannot be a large percentage — or nonbreeding adults do not move south at all to moult. There were no recoveries of tagged seals from Greenland in March and April but this could have been due to chance, especially for Gulf seals, fewer of which were marked. The question is receiving further investigation; several jaws taken at West Greenland settlements in

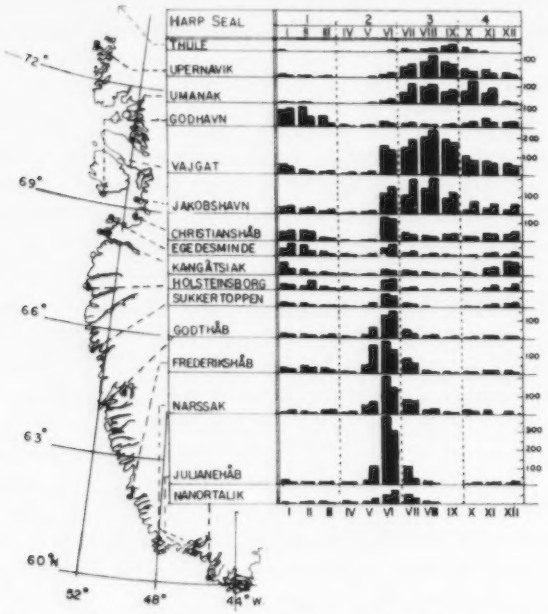


FIG. 6. Catches of harp seals on the west coast of Greenland, 1948 to 1951, by district and half-month. Modified from Rosendahl (1961).

March and April of 1963 and sent to the writer were indeed of immature harp seals.

The recaptures have shown that harp seals of the western stock spend the summer along the whole west coast of Greenland. Whether they also extend round Cape Farewell, as suggested by Nansen (quoted by Jensen, 1928), has not been determined from this limited marking. The coast is an uninhabited one. Small-scale marking of the central stock of harp seals by Norwegian investigators in 1953 (Rasmussen, 1957) showed a drift of young southwestward from the West Ice breeding ground (at 75°N, 5°E approximately) in Denmark Strait towards north Iceland. It seems most likely that Cape Farewell marks the approximate boundary of the two populations. These have breeding seasons separated by approximately 1 month, and show significant differences in body and skull dimensions (Khuzin, 1963; Ïablokov and Sergeant, 1963).

On the Canadian side, L. Tuck (unpublished MS, Canadian Wildlife Service) observed a westward migration of harp seals in Lancaster Sound from Cape Hay, Bylot Island in 1957. There were four observed waves between June 26 and August 2. The last and biggest wave came in late July. In all, some 150,000 seals were counted passing this site westward. Tuck recorded no return movement up to August 23. In the region of Navy Board Inlet on August 22, harp seals were moving into the inlet; on August 23, moving north out of it again. Mr L. Henneberry of the Canadian Department of

Transport on board C.G.S. *Labrador* in 1962 recorded (personal communication) schools of harp seals in Lancaster Sound as late as October 2–4, and A. W. Smith, also on *Labrador*, estimated 10,000 harp seals sighted east of Devon Island at 76°01′N, 77°W on September 28, 1963.

SOUTHWARD MIGRATION

The majority of harp seals pass down the Labrador coast in late autumn, being taken in net fisheries at the present time at Port Burwell, near Cape Chidley, at Nain in mid Labrador, and at La Tabatière and other localities in the northern Gulf of St. Lawrence.

The exact time of migration varies considerably from year to year at least at the more northern localities. In 1963, the fishery at Port Burwell in northernmost Labrador took place between October 17 and November 29 when freeze-up occurred, the largest number of seals being taken on November 27 (Fig. 7, upper part). At La Tabatière, one of the most southerly points

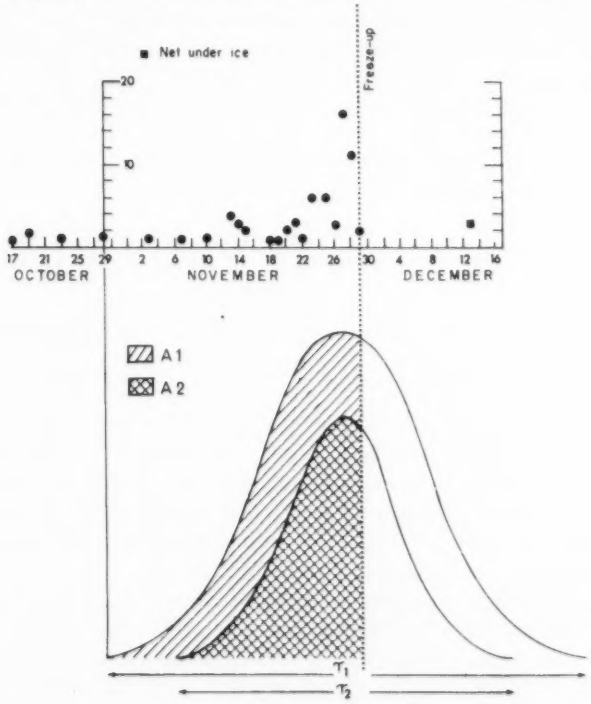


FIG. 7. (Upper) Seals taken at Port Burwell, N.W.T. by net trap, 1963. Data from Canada Department of Northern Affairs and National Resources. Early recoveries were of young animals only and may have been summering animals; later recoveries were of adults and young. (Lower) Idealised curve showing supposed distribution in time of southward migrant harp seals at any one locality. In curve A2, numbers of seals are supposed to be reduced to half those shown in curve A1.

where seals are taken in the autumn net fishery, the first seal was taken on December 18, 1963, and the fishery here continued till about December 29 when it was cut off by early formation of slob ice. Big catches toward the end of these fisheries show that, although the nets must be lifted when the ice comes, the bulk of the seals move south just ahead of local freeze-up; apparently they strongly avoid the slob ice.

The spread of dates given above, with only 20 days between the last seal caught at Port Burwell and the first at La Tabatière, 900 miles (1400 km) distant with the distance measured cape-to-cape, shows that the seal population is widely spread on this migration. Probably, the numbers passing at any one point fall on a normal curve of distribution (Fig. 7, lower part). Local freeze-up cuts off the second part of the curve. Actual catches are of course affected by weather. Reports have been received that the migration has become later since about 1950 in mid Labrador without any change in the date of freeze-up (H. A. Williamson of McGill University Department of Geography, unpublished data). If this is the case, it could be explained by the fact that the numbers of the seals decreased by about half between 1950 and 1960 (Sergeant, 1963). If the area of the normal curve is correspondingly reduced by half, the arrival of the first seals would be several days later than previously (Fig. 7, lower part).

A formal model would be as follows. The population is given by the area (A) contained within the normal curve. This is:

$$A = \sum_{0}^{\tau=4} \frac{1}{2\pi} e^{-\frac{\tau^2}{2}}$$

where τ is the standard measure of the abscissa (Snedecor 1959, p. 204). Since for the smaller population $A_2 = \frac{A_1}{2}$, it will be clear that if $\tau_2 = 1$, $\tau_1 = \sqrt{2}$, or 1.414 approximately. Thus, examining Fig. 7 upper part, if the effective period of migration (excluding earlier immatures) is taken as 19 days, and netting is taken to end 2 days after the peak, the first half of the migration, or normal curve, lasted 17 days. If the population had been twice as great, the first half of the migration would have lasted $17 \times \sqrt{2}$ days or about 24 days, i.e. it would have started a week earlier.

Other explanations are, however, possible for this phenomenon.

Immatures, particularly the youngest age groups, tend to lag behind the main herds. Their relative absence is shown in age samples from Labrador and the northern Gulf (Fig. 8). At an age of 4 or 5 years (the age of sexual maturity) all are represented. This is confirmed by tag returns. There were five recoveries of immature seals from West Greenland in January and February, referring to three young-of-the-year, one second-year and one fifth-year animal (Fig. 5). The localities range from 65° to 70°N, which agrees with catch statistics for Greenland at this time (Fig. 6). At the same time, in December and the first week of January, there were three recoveries of

immature seals from Labrador (Hebron, Nutak, and Kaipokok Bay) and one from northernmost Newfoundland (Cape Bauld). Of these, the animal from Kaipokok Bay was the only seal which had been tagged in the Gulf. The picture is of a wide scattering of immature seals at this time.

No tags were recovered from southward migrant seals at La Tabatière in the Strait of Belle Isle, where the net fishery takes some 1000 harps annually. Thus the tagging provides no evidence as to whether the southward migrant seals separate into their constituent subpopulations on approaching Belle Isle, as claimed by old sealers (Chafe, 1923), or remain mixed until near whelping time. Some seals pass east of Newfoundland, but catches are and have always been relatively small and variable, since the seals pass further out from shore. Most regular catches are made in the neighbourhood of Twillingate. Here in 1952 when the writer spent 3 weeks at the settlement some 60 harp seals were netted in the period January 1–10, with a second movement between January 18 and 22, from which only three were netted; a few were netted at

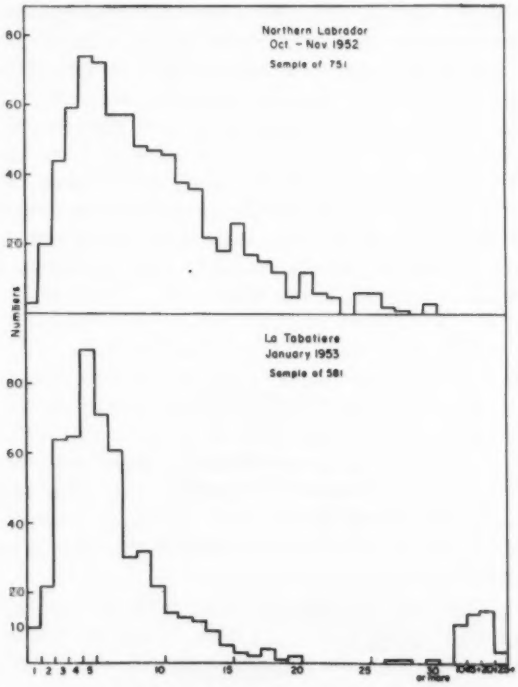


FIG. 8. Two age samples of shore-caught harp seals taken on the southward migration in the same year. The upper sample is a combination of samples from Hebron, Nutak, and Nain, Labrador; the lower from La Tabatière in the northern Gulf. Note the relative absence of immatures, especially of the youngest ages.

Fogo and Change Islands in the same month. Chafe mentions a rare large catch in Bonavista Bay in January 1792, with onshore winds.

Since the above was written, a large number of young seals have been tagged in the Gulf of St. Lawrence just before the start of the spring hunt of March 1964. This was a capture-recapture experiment and will be described in a study on populations. Relevant to the present study is that future recoveries may be expected from the estimated escapement of 1300 young seals. Another new development has been an intensification of netting on the northeast coast of Newfoundland, caused by high prices for seal pelts (information from Mr J. C. Grieve of Bowring Brothers Ltd., Newfoundland). There is therefore a good chance that more light will be thrown on the dispersal of Gulf-born seals on their southward movement. The parallel experiment, a large-scale marking of young seals of the Front herd, remains to be carried out.

WINTERING

Very little is known about the behaviour and whereabouts of the adult-immature population during the period between the southward movement in early January and the movement of the adult females to breeding ice in mid February, except that they are not normally in contact with ice at this time. The lack of reports may be due partly to the scarcity of small boats at sea in January–February when risk of icing is high in the subfreezing air temperatures. We have verbal reports of harp seals from the St. Lawrence estuary in January (Captain Harold Marø of M.V. *Theron*). In 1950 a lighthouse keeper at St. Lawrence, in the Burin Peninsula of Newfoundland, replying to a questionnaire on harbour seals issued by the Fisheries Research Board of Canada Biological Station at St. John's, Newfoundland, described seals black or grey in colour passing westward in February. On February 3, 1962, observers of the Department of Transport on board C.G.S. *Labrador* and its helicopter observed and photographed 300 harp seals on ice forming in Cabot Strait. The majority were described as showing the adult pelage. Evidently, then, adult seals are present in the Gulf of St. Lawrence and its approaches at freeze-up, and mount pack ice as soon as it is formed.

East of Newfoundland there is a complete absence of first-hand reports from at sea, but a few come from coastal locations. Thus radio reports described seals passing the mouth of St. John's harbour northwards on February 24, 1952, and Cape St. Francis in large numbers at the same time, as well as Cape Spear and Ferryland to the south.

Presumably, then, old reports that harp seals winter on the Grand and neighbouring Banks (Robinson, 1897; Chafe, 1923) are substantially correct, though it is surprising that the numerous fishing ships (including research ships) of the present day do not report them. For the most part the seals must keep well offshore.

BREEDING

The segregation of Gulf and Front herds as breeding stocks is based on the following evidence: (1) About the same relative catch is taken out of the

two areas annually, so that the relative stock sizes appear to be constant (at about two to one between Front and Gulf herds). (2) The seals whelp in the Gulf even in exceptional years when pack ice is virtually nonexistent, using ice drifted against the shore, as seen in 1953 (Fisher, 1954). (3) Breeding in the Gulf is on the average some 5 days earlier than on the Front. Figure 9 shows the sequence of whelping for several successive years, as observed by researchers, or deduced from ages of young found.

The relatively small earlier tagging program left no tags to be found on breeding females 4 or more years in age. Thus there is no direct evidence on whether seals born in one area migrate back to breed in it, though there is evidence from tag recoveries that the immatures return to the same areas to shed their hair (see next section).

Figure 10 shows positions of breeding patches as seen from aerial surveys in 1959 and 1960. Positions may change rapidly with drift of the ice. In the past, positions given were necessarily those found by sealing ships. Today, locations may be found by scouting plane somewhat sooner after formation of the patch, so that positions on the Front will tend to be further to the north. Climatic amelioration has probably shifted positions still further northward, and whelping off Hamilton Inlet is now quite common. In the Gulf, whelping patches formed north of the Magdalen Islands are frequently drifted westward and southward to between the Magdalen Islands and Prince Edward Island.

There are frequently two main patches of breeding seals formed on the Front, one or occasionally two in the Gulf. Subsidiary patches are also typical (Fig. 10). Here whelping may occur late, that is, well into March.

The females form up into whelping groups on the ice some 10 days to 2 weeks before whelping, that is in mid to late February, and drift on the ice

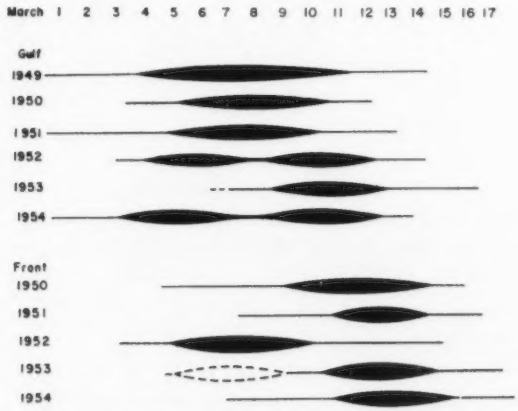


FIG. 9. The time sequence of breeding in the Gulf and on the Front in several consecutive years, as determined from observations and from weights of young sampled.

with the wind and current. Breathing holes must be made when they first haul out.

On the Front, breeding takes place on flat, medium-sized floes of winter ice grading into ice having old pressure ridges which may be older than 1 year. These may or may not be frozen together into large complex floes (Fig. 11). Since the seals penetrate to this ice through open water leads, the freezing together of the floes must be a few days or weeks old only. The seals do not or cannot enter unbroken pack ice further to the north. After arrival on the breeding ice, the seals make breathing holes as long as the leads remain frozen.

In the Gulf, the winter ice is usually made up of large flat floes, sometimes several miles across, with pressure ridges only at the margins or cracks (Fig. 12). The seals frequently make breathing holes through the floes which shows that they colonise the ice when it is very thin. In 1953, the seals found no pack

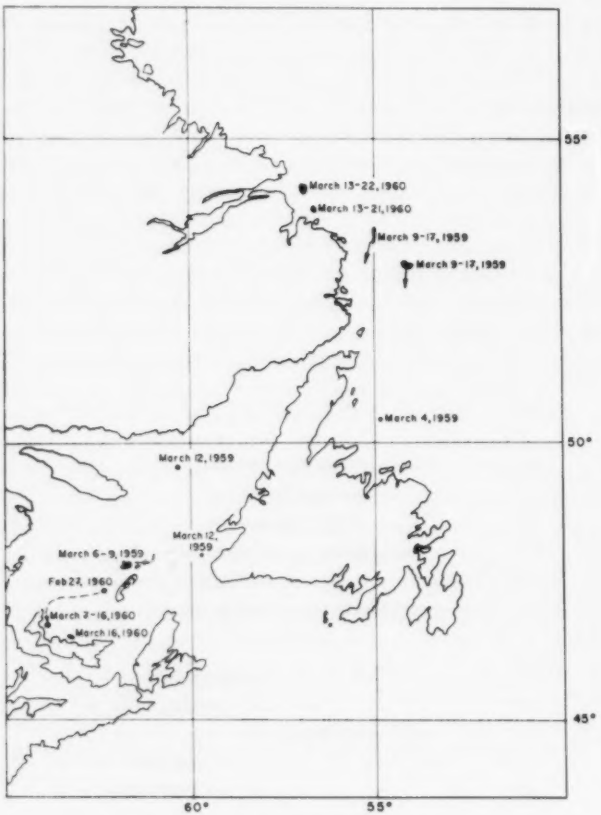


FIG. 10. Breeding locations of harp seals in the Gulf and on the Front in 1959 and 1960. The area of each breeding patch is drawn approximately to scale, and the direction of drift indicated.

ice and whelped on small floes of brash or pancake ice frozen together on the north shore of the Magdalen Islands (Fisher, 1954).

In any one breeding group, births appear to take place through about a week (Fig. 9). Suckling of newborn young is frequent, and the females do not

FIG. 11. Part of a breeding group of harp seals on typical pack ice of the Front, east of Belle Isle, March 13, 1960. Note the rough ice with leads frozen together. (Aerial photo by Hunting Survey Corporation Ltd, Toronto, Ont.)

leave the young at first. As the young becomes larger, the mother leaves it for periods of hours and if the patch is located over shallow water, as often occurs in the Gulf, may take some food of bottom organisms. The problem

FIG. 12. Part of a breeding group of harp seals on typical pack ice of the Gulf of St. Lawrence, March 6, 1959. Many of the animals close to the thinly frozen water leads are without pups. (Aerial photo by Atlantic Aviation Ltd, Halifax, Nova Scotia.)

FIG. 13. Breeding adult females, one showing the threat posture. Gulf of St. Lawrence, March 1954. Photo by the author.

arises of how the young animal is found again. Adult females have an "individual distance" or small territory and display at each other by raising the head and neck vertically (Fig. 13) and growling. Thus a mother with a pup will drive away a strange female looking for its pup. On the Front in 1953, there was a gale on the opening date of sealing, March 10. The author was able to watch undisturbed seals close to the ship. Mothers and small young were seen to carry out much mutual "nosing." Supposedly, the mother may learn to recognise her pup by olfaction. Alternatively, voice may be important. Possibly, then, by a trial and error search, and by olfactory or auditory recognition at close range, the female eventually regains its pup on the drifting ice.

A few days after birth, in mid March, the adults mate. The males have been in the vicinity, in groups either close to the groups of breeding females or at times actually among them. The males enter the water readily when disturbed but their strong musky odour is detectable (information from Dr A. W. Mansfield). Mating may take place in the water or on the ice; the latter occurs when the ice is packed tightly together and the seals cannot enter the water.

MOULTING

The moult or hair shedding of adults and immatures, 1 year and older, begins on the ice in late March, and continues into May, grading into the northward migration. A sequence of moulting locations and dates for 1 year, 1962, is shown in Fig. 14.

Ten recaptures of tagged seals come from seals moulting on the ice fields on the Front between late March and mid May (Fig. 15). All had been marked in this area as young. There were no recoveries elsewhere at this time. They refer to animals 1–4 years of age (Table III). By this time, therefore, the immatures of the Front herd, or at least the very great majority of them, have passed south and joined the herds of adults.

Rasmussen and Öritsland (1964) give details of 14 recoveries of 97 young harp seals tagged by Norwegian investigators on the Front in 1951 and 1952. Twelve were recaptured within 6 weeks on the Front, and two on the Front during April of subsequent years at ages of 1 and 3 years. These results should be added to those reported here.

A single recapture in the Gulf of St. Lawrence is of a seal marked in the Gulf 2 years before. Because the ice fields disappear early in April in the Gulf, relatively few moulting seals are taken there by ships. Some are taken by landsmen around the southern Gulf, especially in a hook-and-line fishery from the Magdalen Islands in April and May.

At one time it was believed possible that some of the Gulf seals moved to the Front to moult. The above recoveries make this unlikely. Other contrary evidence is as follows:

(1) In an aerial survey of moulting seals carried out in April 1962, the ice in the Strait of Belle Isle was thoroughly searched for harp seals but none was found. All moulting patches lay at the eastern edge of the ice east of Belle Isle (Fig. 14), and were presumably Front seals.

FIG. 14. The sequence of moulting locations in the Gulf and on the Front in 1962, with an extension in the Gulf for 1963, as determined from aerial reconnaissance and ships' catches.

Mr Karl Karlsen of Karlsen Shipping Company Ltd. states that his sealing ships find and shoot moulting seals in the northern Gulf of St. Lawrence just north of the 50th parallel of latitude during late April. We have not found these seals in our aerial surveys, which may not have been extended far enough south from the Strait of Belle Isle. We suppose that, with the disappearance of ice in the middle of the Gulf of St. Lawrence during April, moulting animals retreat following the ice fringe both to the southern and northern Gulf.

(2) Statistics received from the Bureau of Statistics, Department of Trade and Commerce of the Province of Quebec show the catch of harp seals in the first 6 months of 1962 from the north shore of the Gulf of St. Lawrence (Table IV). Catches in January show the southward migration of adults and immatures. Catches of young in March and April are of Front-born seals, drifted into the Strait of Belle Isle and close to shore by wind and current action. Catches in May and June show the adults and immatures of the Gulf herd passing out mostly in May, the young mostly in June. An age sample from Blanc Sablon taken in June 1957 showed nearly all young seals of the year (Fig. 4). No other age samples have been obtained from the spring migration; netting on the Labrador coast in spring is less intensive than in autumn since there is no natural refrigeration to preserve meat and pelts.

(3) The seals may pass out also on the Newfoundland side of the Strait of

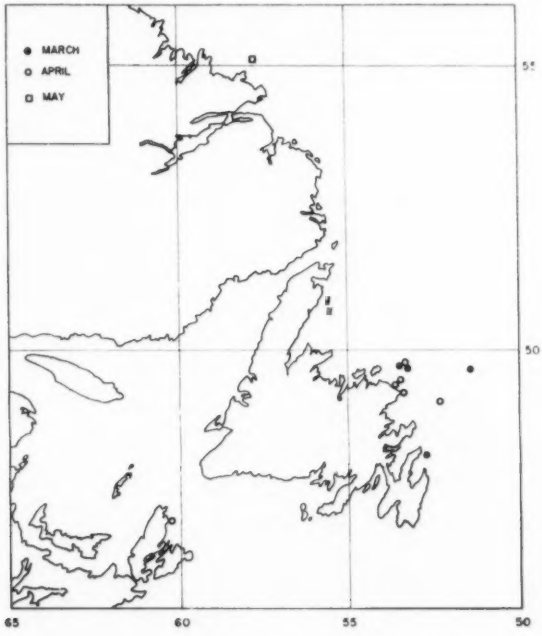


FIG. 15. Recaptures of young harp seals at the moulting patches in subsequent years, all in March, April, and May.

Belle Isle. Thus, in 1952, reports were received of thousands of seals passing Brig Bay to Big Brook area between May 20 and June 15. Few were netted, although they passed close in to the coast (local radio report noted by Mr G. M. Drover).

Little can be said about the course of moulting in the Gulf. Normally, few immature and adult seals are taken from ships so that sampling from this source has not been possible. A photographic survey of the moulting patches in the Gulf in the first half of April 1962 gave a count of at least 23,000 adults (identified by their saddles) out of 30,000 seals on the ice. Age samples obtained

TABLE V. Age and sex composition of moulting harp seals.

			Males				Females				
Year	Ship	Date(s)	1–5 yr	6 yr	Total	Over 5 yr	1–5 yr	6 yr	Total	Over 5 yr	Males
			no.	*no.*	*no.*	*%*	*no.*	*no.*	*no.*	*%*	*%*
1952	*Blue Seal*	Apr. 10–12	12	38	50	76	7	5	12		81
		Apr. 17	11	31	42	74	4	8	12		72
		Apr. 20–22	22	61	83	73.5	15	9	24		78
1953	*Algerine*	Mar. 28–30	37	21	58	36	40	–	40	0	59
1953	*Theron*	Mar. 28	5	11	16	70	1	2	3	(N.S.)	(84)
		Apr. 6	8	1	9	(10)	2	0	2	(N.S.)	(81)
		Apr. 14	28	36	64	56	33	5	38	13	63
		Apr. 18	140	144	284	51	98	17	115	15	71
		Apr. 22–23	107	159	266	60	66	51	117	44	70
		Apr. 27–28	25	72	97	75		3748	85	56	53
1954	*Theron*	Mar. 29–31	'36	24	60	40	27	1	28	4	68
		Apr. 6	66	6	72	8	42	3	45	7	62
		Apr. 10–14	37	40	77	52	48	4	52	8	60
		Apr. 17–21	28	43	71	61	24	8	32	25	69
		Apr. 22–24	20	53	73	73	8	35	43	81	63
1962	*Theron*	Apr. 11–12	146	18	164	11.0	109	9	118	8	58
		Apr. 19–21	161	75	236	33.8	145	8	153	5	61
		Apr. 26–28	38	37	75	49.3	35	31	66	47	53

from the Magdalen Islands in 1956 and 1957 through Mr Paul Montreuil of the Quebec Department of Fisheries showed a relative absence of immatures (Fig. 4). These samples were mostly taken from a hook-and-line fishery in April and May, at a time when the seals are feeding heavily on fish, especially herring (*Clupea harengus*) (Fisher and Mackenzie, 1955; Myers, 1959). Whether part of the immatures of the Gulf herd remain in West Greenland waters, or remain segregated from the adults within the Gulf, possibly taking different food, cannot be determined from the available data.

On the Front, much sampling of moulters has been possible from Canadian sealing ships. Changes in age–sex composition with the season are shown in Table V and analysed in Fig. 16–18. The situation is as follows: The first-formed patches in late March are composed of immatures of both sexes and adult males in separate patches, as shown by marked variations in the percentage of adult males (Fig. 16). Later, these mix to show a more steady composition. Adult females enter more gradually (Fig. 17) and become fully represented only by late April, when they represent about half of all females (Fig. 17), and the females represent half the total moulters (Fig. 18).

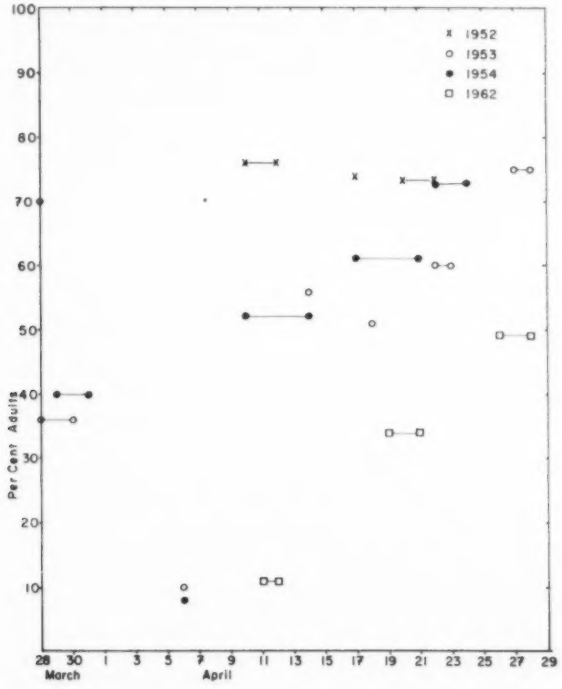


FIG. 16. The moulting sequence of male seals on the Front. Adult males as per cent total males.

Most samples taken from Canadian sealing ships on the Front have shown a greater abundance of young age classes than would be expected from mortality rates (Fig. 19). This is true even for the males alone, in which the adults are present throughout the moult. The reason appears to be that the immature age classes moult on the whole in the most southerly-lying ice, the adults further north. The thinner, southerly-lying ice is more easily penetrated by the ships.

Statistics of catch by Norwegian ships formerly separated categories of immature and adult seals by pelt type. They showed a greater percentage of old seals in their catches than did Canadian ships on the Front. The reason seems to be that the Norwegian ships tend on the whole to work the ice fringe further north, and before agreement as to a closing date, tended to seal for a longer period than the Canadian ships. The difference in catch composition would be explained by these spatial and temporal differences in sampling a stock of seals showing the cline of age and sex composition discussed above.

The separation of immatures and adults was most clearly marked in 1962, when the ice was at first separated into northern and southern regions by open water. Groups composed largely of adults (saddle seals) were observed

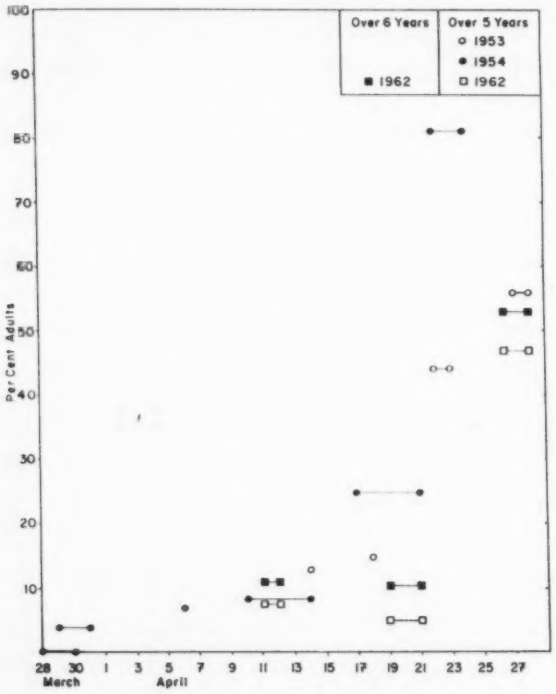


FIG. 17. The moulting sequence of female seals on the Front. Adult females as per cent total females.

and photographed by aircraft off the eastern Labrador coast in mid to late April, while at the same time groups made up largely of younger seals — mostly 1- and 2-year-olds — were sampled from shipboard further south (Table V; Fig. 19). These groups had largely coalesced by April 26, with adult females added in.

In 1962 it was striking that the first-formed patches of adult seals formed only a few miles east of the breeding patches; the adults were beginning to haul out on April 5 while sealing ships were still cleaning up a nearby patch of young. The composition of these adults, whether males or females or mixed, was unknown since no ships sampled them.

Considering other years also, the simplest explanation of the rather complex variations in age–sex composition of the moulting patches on the Front is that the adults, probably old males alone, tend to begin the moult in the neighbourhood of the site of the breeding patch in late March; this may have drifted considerably southward or may not. At the same time the immatures begin to moult at the southern extremity of the ice. The adults drift south for a while, the immatures move north, both mix and begin to move north

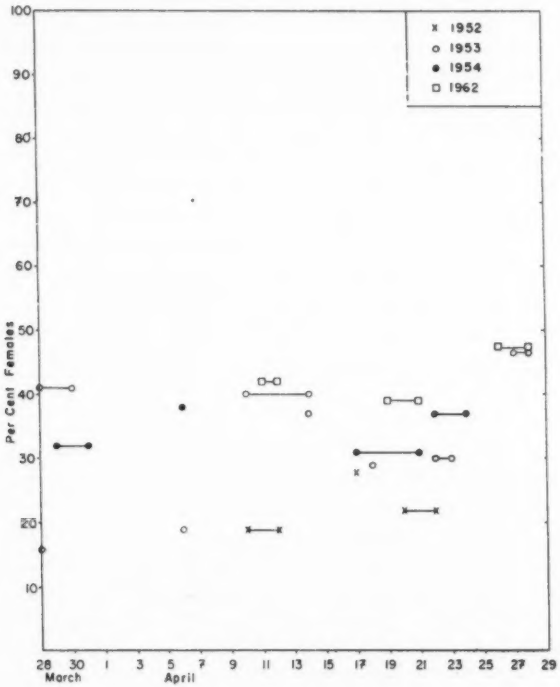


FIG. 18. The moulting sequence of seals on the Front. All females as per cent of all seals.

more actively. The adult females, which have been absent on an unknown ground, join the mixed herds.

The seals are said to avoid the broken-up pack ice close to the outer ice edge where they will presumably be killed by ice grinding when in the water. In the aerial survey of 1963, it was noticeable that during a period of dull weather and northeast winds between April 20 and 25, when the swell was churning up the ice edge, the patches of moulting seals all lay 8 km or more inside the ice edge. By contrast, during the same period in 1962, when westerly winds and sunny skies prevailed, the seal patches lay close to the outer ice edge.

The spring movement has been traced as far as Nain, Labrador, where the seals are said to enter close into the bays after a small capelin-like fish (probably young capelin, *Mallotus villosus*) just after breakup of the fast ice in June or July. They are then said to be very lean.

The seals reaching the inshore part of the Labrador coast at this late date cannot be the main wave which reaches West Greenland by early June.

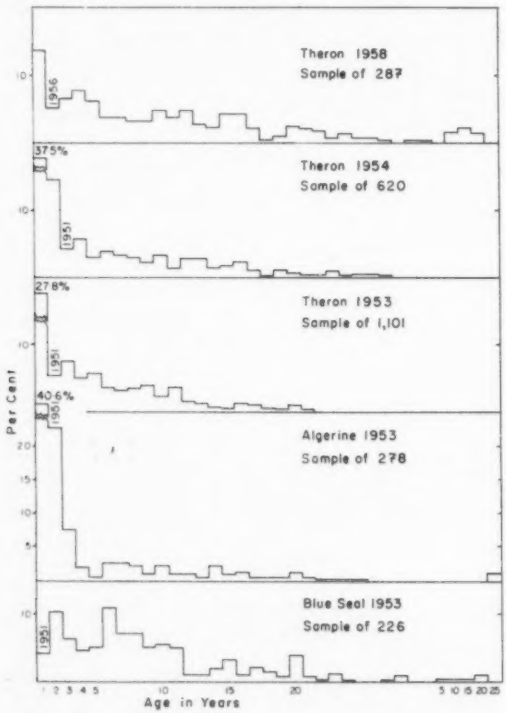


FIG. 19. Age samples of moulting harp seals from the Front, sampled from different ships in different years.

Presumably the main mass of seals passes along the outer border of the ice of the Labrador Sea and Davis Strait to reach the West Greenland coast.

Thus the evidence suggests that the two herds of harp seals retain their identity as breeding and as moulting animals, in spite of complete mixing on their summer range, and for at least part of their northward and southward migrations. The fact that the Gulf herd moults in the Gulf seems remarkable considering that the ice in the Gulf has almost vanished by late April or early May. However, a plausible explanation lies in the fact that the Strait of Belle Isle is blocked with drift ice from the Front, irregularly but frequently and for several days at a time, until well into May (e.g. May 14–16, 1962, see Archibald *et al.*, MS, 1962). Seals in the water in the narrow part of the Strait would be killed by ice-grinding, as at the ice margin. Presumably, then, selection has produced a delay in migration of Gulf seals until the Straits are regularly free of close ice.

This hypothesis would be invalidated if the relatively few adult hood seals, *Cystophora cristata* Erxleben, which breed in the Gulf of St. Lawrence should pass out through the Strait of Belle Isle in late March and early April, which is the period when the hood seals breeding on the Front leave the young and move northward. An alternative hypothesis for the harps has been suggested to me by Mr Rene Jones, of Harrington Harbour on the North Shore of the Gulf, who is familiar with sealing in this district. He points out that the moulting harps may merely swim northward till they meet the first ice, which in mid April will be in the northern Gulf. They then rest on the ice which as on the Front has a net southward drift. In this way their passage through the Strait of Belle Isle is delayed. Mr Jones suggests that some harps may pass out earlier than May or June. The statistics of catch in the northern Gulf and the Straits, however, do not suggest that many seals pass close to shore earlier than May.

The existence of two distinct stocks of harp seals, breeding and moulting in the Gulf of St. Lawrence and on the Front, respectively, is important in the management of the seal fishery. Population dynamics of these stocks will be discussed in a separate paper.

SUMMARY

1. Young harp seals after weaning show three successive movements: (1) an active movement out from the ice where they were born to the ice border where they begin to feed at 4–6 weeks, (2) a passive drift in the current, and (3) an active migration northward at 8–10 weeks. The orienting mechanisms of the two active movements are unknown. At this stage the animals are solitary. The young migrate northward separately from and somewhat later than the adult and immature schools.
2. During the summer months harp seals of the northwest Atlantic population extend from Thule, Greenland, and Jones Sound between Devon and Ellesmere Islands south to northern Labrador waters, and from Cape Farewell west to northwest and southeast Hudson Bay.

3. The southward movement begins in October and reaches the Strait of Belle Isle in late December. The adults and a percentage of immatures, decreasing with decreasing age, move at this time. The remainder of the immatures move south later. The great majority of immatures of the Front herd is represented at the moulting grounds in April, though many of the Gulf immatures are not accounted for even at this time. Some immatures may remain permanently in West Greenland waters.
4. Wintering areas and behaviour in January–February are still virtually unknown.
5. Harp seals separate into two groups, in the Gulf of St. Lawrence and east of Newfoundland ("Front" area) to breed. The groups are relatively constant in location, numbers, and breeding date annually, suggesting that they are distinct.
6. Moulting begins shortly after breeding is ended. Seals east of Newfoundland moult largely on the ice; seals in the Gulf of St. Lawrence, mostly in the water. Moulting groups east of Newfoundland at first consist of immatures and adult males, the immatures further to the south, which gradually mix during April. Adult females which have given birth join these groups later and all age-sex classes are represented by late April.
7. Ten seals tagged on the Front as young were recaptured moulting on the Front 1–4 years later. One seal tagged in the Gulf was recaptured in the Gulf 2 years later, suggesting constancy of return to the home area by the immature seals. Since seals breeding in the Gulf of St. Lawrence do not leave the Gulf until May, the adults also must moult in the Gulf and cannot mix with the Front herd until well into the northward migration.

ACKNOWLEDGMENTS

Tagging with Canadian tags was carried out by Dr H. D. Fisher and by the Norwegian investigator Per Høst in 1950; by Fishery Inspectors Thomas Reddy and R. L. Stevenson in 1951; by the author assisted by John Clowe as well as by Philip Knowling and Thomas Reddy in 1952; by Fisher assisted by B. A. Mackenzie, and by the author assisted by Charles Rose in 1953; and by the author and Charles Rose in 1954. I am particularly grateful to Dr Fisher, and also to Dr P. M. Hansen, head of the Greenland Fishery Investigations of the Danish Government, for providing much information in unpublished material and in discussion over a number of years. Thanks are due also to Mr Paul Montreuil of the Quebec Department of Fisheries for providing age samples from the Magdalen Islands, to Mr Karl Karlsen of Karlsen Shipping Co., Mr Max Budgell of the Department of Northern Affairs and National Resources of Canada, Mr W. Rockwood of the Division of the Northern Labrador Affairs, Department of Public Welfare of Newfoundland, and Mr Ph. Rosendahl of the Greenland Administration of the Danish Government for providing other age samples. Observers on ships and planes of the Canada Department of Transport contributed many observations of seals on

questionnaires supplied by the Arctic Biological Station. Mr G. S. Drover also contributed much interest to this work in its early stages, and Mr James Grieve has long provided stimulating discussion. Mr T. R. Welch assisted by Mr John Christopher collected samples in 1962 and also made many of the illustrations of this paper. Mr Rene Jones and Mr Brian Beck collected material from the Quebec North Shore in December 1963 and provided observations on this part of the seal migration. My colleagues Mr J. G. Hunter and Dr A. W. Mansfield of this Station provided valuable advice and criticism.

REFERENCES

ALLEN, J. A. 1880. History of North American pinnipeds. U.S. Govt. Printing Office, Washington, D.C.

ARCHIBALD, D. C., M. N. MONSINGER, AND T. B. KILPATRICK. MS, 1962. Aerial ice observing and reconnaissance, Eastern Canadian Seaboard, 1962. *Met. Branch, Dept. Transport, Canada*, CIR 3768, Tec. 438, 3 December, 1962.

ARMSTRONG, T., AND B. B. ROBERTS. 1956. Illustrated ice glossary. *Polar Record*, **8**(52): 4–12, 40 fig.
1958. An illustrated ice glossary. *Ibid*, **9**(59): 90–96, 30 fig.

CHAFE, L. G. 1923. Chafe's Sealing Book: A history of the Newfoundland seal fishery from the earliest available records down to and including the voyage of 1923. H. M. Mosdell [ed.], 3rd edit., St. John's, and annual supplementary sheets up to and including 1952 (issued from 1940 by Newfoundland Fisheries Board), 105 pp.

CHAPSKY, K. K. 1961. Nekotorye ekologicheskie obosnovaniia sezonnoi dinamiki areala belomorskoi populatsii grenlandskogo tiulenia (*Pagophoca groenlandica*). [Some ecological factors determining seasonal changes in distribution of the White Sea harp seal population (*Pagophoca groenlandica*)] *Trudy Soveshchanii Ikhtiologicheskoi Komissii Akad. Nauk S S S R*, **12**: 150–163. [FRB Translation Series No. 380.]

FISHER, H. D. MS, 1954. Studies on reproduction in the harp seal *Phoca groenlandica* Erxleben in the Northwest Atlantic. Ph.D. thesis, McGill University, Montreal, Que.

FISHER, H. D., AND B. A. MACKENZIE. 1955. Food habits of seals in the Maritimes. *Fish. Res. Bd. Canada, Prog. Rept. Atlantic Coast Station*, No. 61, pp. 5–9.

HUNTSMAN, A. G., W. B. BAILEY, AND H. B. HACHEY. 1954. The general oceanography of the Strait of Belle Isle. *J. Fish. Res. Bd. Canada*, **11**(3): 198–260.

IABLOKOV, A. V., AND D. E. SERGEANT. 1963. Izmenchivost' kraniologicheskikh priznakov grenlandskogo tiulenia (*Pagophilus groenlandicus* Erxleben, 1777). [Cranial variation in the harp seal (*Pagophilus groenlandicus* Erxleben, 1777).] *Zoologicheskii Zhurnal*, **42**: 1857–1865. [FRB Translation Series No. 485.]

JENSEN, AD. S. 1928. Grønlands Fauna. *In* Københavns Universitets Festskrift, 26 November.

KHUZIN, R. SH. 1963. Materialy po morfologicheskoĭ kharakteristike trekh stad grenlandskogo tiulenia *Pagophilus groenlandicus* Erxl., 1777. Materialy rybokhoziastvennykh issledovaniĭ severnogo bassenia. *Sbornik* No. 1, PINRO, pp. 51–54, Murmansk, 1963.

MYERS, BETTY J. 1959. The stomach contents of harp seals (*Phoca groenlandica* Erxleben) from the Magdalen Islands, Quebec. *Canadian J. Zool.*, **37**: 1 p.

RASMUSSEN, B. 1957. Exploitation and protection of the East Greenland seal herds. *Norwegian Whaling Gazette*, **2**: 45–59.

RASMUSSEN, B., AND T. ÖRITSLAND. 1964. Norwegian tagging of harp seals and hooded seals in North Atlantic waters. *Fiskeridirektoratets Skr.*, **13**(7): 43–55.

ROBINSON, CDR. GEORGE. 1897. Ice-riding pinnipeds. A description of the migration and peculiarities of Phoca Greenlandica and Cystophora Cristata... on the northeast coast of America. London, J. D. Potter, 1897.

ROSENDAHL, PH. 1961. Grønlandsk jagt- og fangststatistik. *Geografisk Tidsskr., København*, **60**: 16–38.

SERGEANT, D. E. 1963. Harp seals and the sealing industry. *Canadian Audubon*, **25**(2): 29–35.

SNEDECOR, G. W. 1959. Statistical Methods. 5th ed. Iowa State College Press, Ames.

SURKOV, S. S. 1960. Dannye po biologii i promyslu lan-maienskovo lysuna i khokhlacha v zapadnykh l'dakh. [Data on the biology and hunting of the Jan-Mayen harp and hood seals in the West Ice.] *Trudy PINRO*, **12**: 88–106. Murmansk.

Trends in Catch, Age, and Size of Cod from the Commercial Longline Fishery at Bonavista, Newfoundland, 1952–62[1]

By A. M. Fleming

Fisheries Research Board of Canada
Biological Station, St. John's, Nfld.

ABSTRACT

A commercial longline fishery for cod was begun from Bonavista in 1952. Catches remained high until 1956, particularly on the deep-water grounds but thereafter decreased rapidly because of (a) the intense fishery, especially by European otter-trawlers and longliners after 1956, and (b) irregular recruitment to the fishery. The decrease in catch per unit of effort was marked by wide changes in the age and size compositions of the catch. The cod in deep-water catches tend to be older and larger than in the shallow-water catches.

INTRODUCTION

As a result of experimental longline fishing carried out by the Fisheries Research Board of Canada in 1950 and 1951 (Templeman and Fleming, 1956), a commercial longline fishery for cod was begun off Bonavista in 1952 (Fig. 1). The highlights of the fishery by longlines and other gears at Bonavista have been reported annually (FRB, 1953–61), and Templeman and Fleming (1956), have outlined some of the results of the earlier years. The purpose of this paper is to report on trends in the catches during the first 11 years of the commercial longline fishery and to examine changes in the age and size compositions of cod in the catch.

METHODS

Information on the catch and fishing effort of most of the boats was obtained by interviewing the captains at the end of each trip. Where this was not possible for a particular boat or trip, the effort was based upon the usual number of lines fished per trip by the boat concerned. A trial of both these methods on boats where effort was known indicated that no serious errors resulted by estimation in the second method.

All cod caught were generally above the minimum size acceptable for processing so discarding was negligible. Length measurements of representative samples of catches were obtained when the cod were landed, with sampling occurring mainly in June to August for the deep-water fishery and in September for the shallow-water fishery. Lengths were measured to the nearest centimetre from the tip of the snout to the mid-fork of the tail, but for the following analysis they were combined in 3-cm groups.

The weights recorded are of fish as sold to the plant, in pounds, head-on, gutted (1 lb = 0.454 kg). The length–weight relationships are based on data

[1]Received for publication January 13, 1965.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

obtained from measuring and weighing several thousand cod from many Newfoundland areas; average weights are the averages at the median of each 3-cm group.

While length measurements of cod were being made, otoliths for age determination were collected from a percentage of the fish measured (Table I). In the earlier years otoliths were collected only from cod selected at random

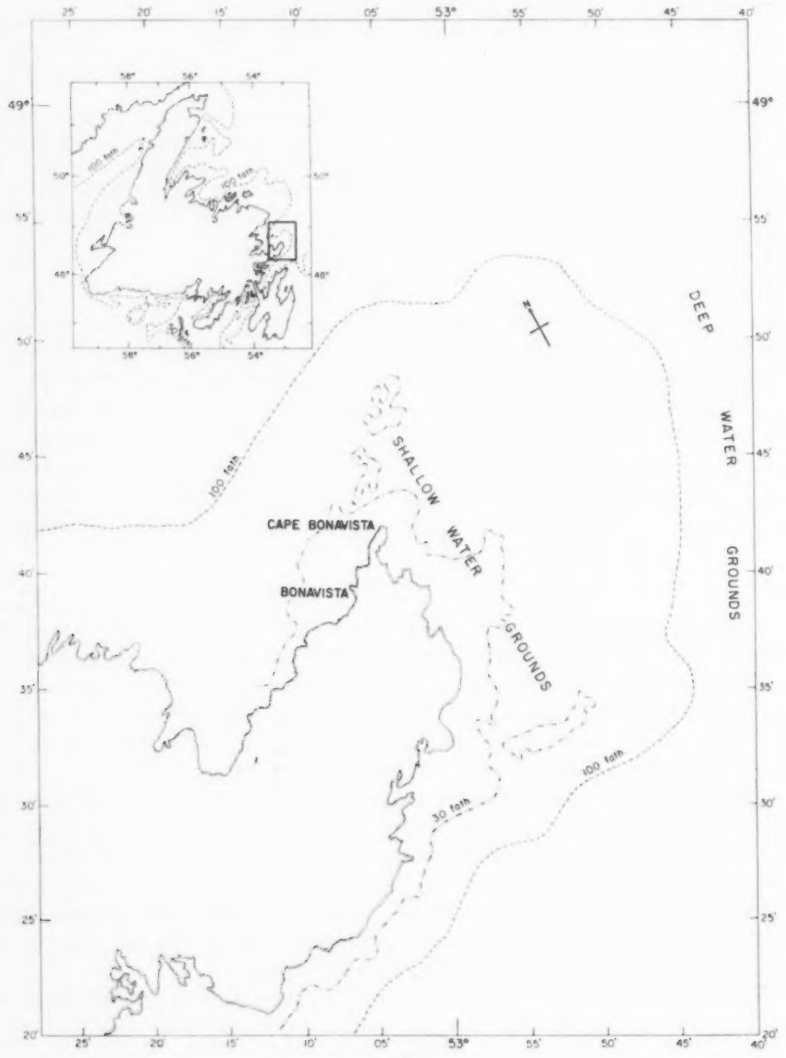


FIG. 1. Map showing the location of the principal longlining grounds off Bonavista.

but in later years the random samples were supplemented by additional fish selected at the smaller and larger sizes. The zonation of cod otoliths in this area is often difficult to interpret and errors of ±1 year in age determination have undoubtedly occurred in some cases. However, otoliths which were difficult to interpret were generally checked by more than one person before a decision on the age was made.

For comparison of the year-to-year results the age, length, and weight distributions in a particular year have been expressed in terms of average catch of the longline fleet per 100 lines of gear fished. However, because of the small number of otoliths obtained in sampling the deep-water fishery in the earlier years, age samples from 1952 and 1953 deep-water catches were combined to make an age–length key from which the age composition of cod in the catch per 100 lines in each of these years was derived. Similarly the age compositions for 1954, 1955, and 1956 were derived from an age–length key based upon the combined age samples for these years. In all other years the age samples were adequate without combination.

In adjusting the age and length frequencies to distributions based upon the catch per 100 lines there were cases in the earlier years in which an occasional fish in the largest sizes in the length sample had not been sampled for age. Ages were assigned in these cases from observation of known ages of fish in the same length range from other years.

TABLE I. Samples used to determine age and length compositions of cod in the deep and shallow longline catches off Bonavista, 1952–62.

	Deep		Shallow	
Year	Lengths	Otoliths	Lengths	Otoliths
1952	2844	137	–	–
1953	1824	93	–	–
1954	1873	92	–	–
1955	1606	119	–	–
1956	2700	171	–	–
1957	6222	491	2900	144
1958	5472	386	–	–
1959	3715	278	–	–
1960	1697	314	1229	121
1961	1140	215	1030	151
1962	1110	230	1403	204

THE DEEP-WATER FISHERY

The area, depth, and temperature relationships to cod catches in the Bonavista area have been discussed fully by Templeman and Fleming (1956, 1962). In 1952 the deep-water stocks consisted of cod which had not been exploited previously except during the fishing experiments in 1950 and 1951 and also when, as younger fish, large numbers of them moved shoreward during summer to the shallower inshore areas where they were fished by codtraps, handlines, and other line gears. Consequently, fishing such an accumulated stock would be expected to yield good catches. The experimental fishing had shown that consistent catches of about 10,000 lb of head-on, gutted cod per 100 lines of gear were indicative of abundant supplies. From 1952 to 1955 the average catch of cod per 100 lines was maintained above 10,000 lb (Fig. 2, Table II). In 1956 the average had dropped to 9510 lb per 100 lines, partly because many of the boats had made more trips in autumn to the inner part of the deep-water area to the northeast of Bonavista (Fig. 1) where catches were not as high as farther offshore. In 1957, however, a further decline occurred, the average catch per 100 lines being 8500 lb, and subsequent years were marked by a steady decline to a catch level about one-third of what it was in the early years of the fishery.

From 1952 to 1957 the deep-water catches per 100 lines of gear were about twice the shallower-water catches. However, the reduction of the catches from deep water occurred at a faster rate than from the shallow grounds so that, in 1961 and 1962, catches from both areas were approximately at the same level.

Figure 3 illustrates the age, length, and weight distributions of the annual deep-water catches as derived from sampling. An examination of these distributions yields additional information on the changes which took place between 1952 and 1962.

During 1952, the first year of the commercial longline fishery, a very high proportion of the catch consisted of large cod averaging 76.4 cm in length

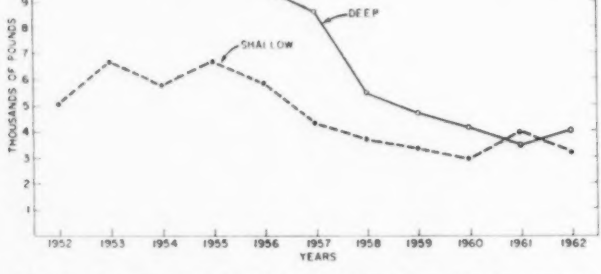


FIG. 2. Average catch of cod (per 100 lines of gear) in the deep and shallow longline fishery off Bonavista, 1952–62.

TABLE II. Summary of information on effort and catch of cod in the longline fishery off Bonavista, 1952–62.

	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962
A. Number of boats fishing											
	9	14	16	10	11	13	13	12	10	8	9
B. Duration of fishery											
Deep	June–Oct.	May–Nov.	June–Sept.	June–Oct.	June–Oct.	June–Oct.	May–Oct.	May–Oct.	May–Sept.	May–Sept.	May–Sept.
Shallow	Aug.–Dec.	Aug.–Dec.	Aug.–Dec.	Aug.–Dec.	Aug.–Dec.	Aug.–Dec.	Aug.–Nov.	Aug.–Dec.	Sept.–Nov.	Aug.–Nov.	Sept.–Nov.
C. Average weight of cod per 100 lines (head-on, gutted in lb)											
Deep	10,464	10,256	10,448	10,111	9,508	8,503	5,461	4,665	4,160	3,473	4,022
Shallow	5,074	6,655	5,758	6,649	5,846	4,237	3,684	3,331	2,983	3,970	3,216
D. Average number of cod per 100 lines											
Deep	1,354	1,459	1,645	1,405	1,592	1,587	992	851	650	554	734
Shallow						1,014			715	926	798
E. Average age of cod (years)											
Deep	13.4	12.5	11.8	12.8	11.4	11.3	11.2	11.4	11.8	11.8	10.0
Shallow						8.9			9.0	7.4	6.9
F. Average length of cod (cm)											
Deep	76.4	73.2	70.5	74.0	69.1	67.3	67.7	67.7	70.9	70.7	67.4
Shallow						61.8			61.8	61.8	60.9
G. Average weight of cod (head-on, gutted in lb)											
Deep	7.7	7.0	6.4	7.2	6.0	5.4	5.5	5.5	6.4	6.3	5.5
Shallow						4.2			4.2	4.3	4.0
H. Range of depths fished											
Deep	100–180	125–180	100–170	100–160	100–180	100–170	100–196	124–180	100–165	100–160	110–160
Shallow	10–100	30–80	15–98	15–80	15–80	5–106	20–80	20–70	10–60	10–60	5–75

and 7.7 lb head-on, gutted weight. The age distribution shows most of these fish to be 12–19 years of age, with ages 12–14 (1940, 1939, and 1938 year-classes) being the most abundant and younger ages being relatively scarce (average age, 13.4 years). In subsequent years up to 1956, catches continued at a high level because of large contributions both in numbers and weights of the older age-groups. In these years the 1938–41 year-classes maintained their dominance. Also, contributions to the catches by the younger age-groups (about 6–10 years, principally the 1947 and 1948 year-classes) were great and became greater between 1953 and 1956, as indicated by a strong mode at the younger and smaller sizes in the age, length, and weight frequencies of the catch samples.

From 1952 to 1956 the age and size structure of the stock changed gradually as the older age-groups were reduced by fishing and natural mortality and the younger age-groups continued to be recruited to the fishery and contribute more heavily to it. In this period the regular decrease in the older fish and the increase in the younger fish are shown more clearly by the length than by the age compositions (Fig. 3). (The age distributions for 1952–56 are somewhat inaccurate because only small age samples were available, which necessitated the use of age–length keys to derive age compositions from the length–frequency distributions.) The change in stock structure was marked by a decrease in the average length and weight of fish in the catch to 69.1 cm and 6.0 lb and a lowering of the average age to 11.4 years in 1956.

In 1957 a continued reduction in numbers of cod in the age-groups over 15 was obvious and the deep-water longline fishery depended for success principally on the younger age-groups, with the 1947 year-class being especially dominant through the years to 1961. Although the younger fish were abundant in this period, because of their smaller size their total contribution in weight to the catch was much less than that earlier contributed by the older age-groups which now were no longer significantly represented in the fishery. This is evident from the rapid decrease in the catch per unit of effort following 1957 (Fig. 2).

Also, following the greatly reduced significance of the older age-groups in the catches, an obvious reduction occurred in the numbers and weight of fish in the dominant young age-groups. The effect on the catch was severe because no other very strong year-classes were recruited to the fishery during this period. In 1961, however, there were indications of some moderately successful groups of young fish being recruited. By this time the somewhat older age-groups (about 9–12 years), which had contributed so heavily in 1957 and 1958, were so reduced in numbers that the end result in 1962 was a decrease in the average age, length, and weight of cod to 10.0 years, 67.4 cm, and 5.5 lb, respectively. However, the contribution of the reduced numbers of the older age-groups together with that from the increasing numbers of the young ones was sufficient to indicate a slight increase in the catch per unit of effort.

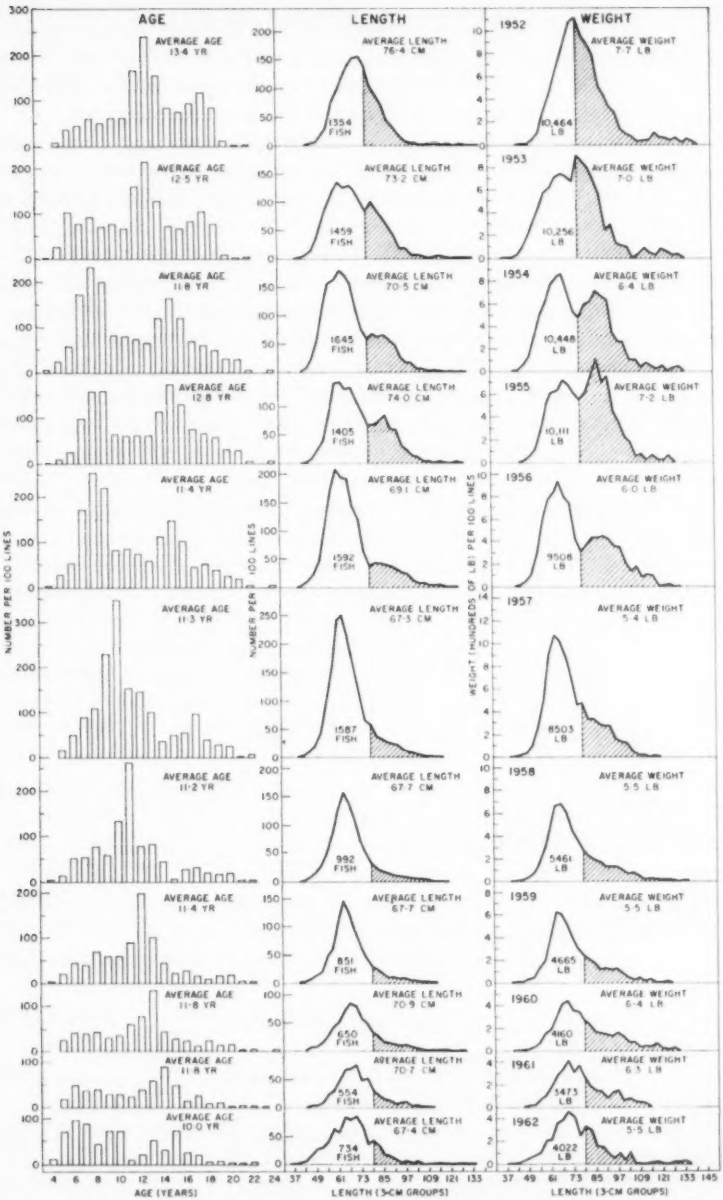


FIG. 3. Age, length, and weight distributions (per 100 lines of gear) of cod in the deep-water longline catches off Bonavista, 1952–62. Numbers of fish in the length–frequency polygons are numbers per 100 lines, weights in the weight–frequency polygons are weights of catch per 100 lines.

THE SHALLOW-WATER FISHERY

The fishery by the experimental longliners in 1950 had established that the yield per unit of effort was generally much lower on the shallow water grounds (in depths less than 100 fathoms) than on the deep grounds farther offshore. For this reason the longliners fished the deep-water grounds as often as possible throughout the season until the autumn, when weather conditions often limited the boats to venturing no farther than the shallow-water inshore grounds (Fig. 1).

Early in the summer, cod in the inshore region inhabit the upper water layers where they are fished by codtrap, handline, and other line gears. By autumn they gradually retreat to somewhat deeper water, down to about 40 fathoms, where they can be fished by the longliners in certain areas, particularly southeast of Cape Bonavista (Templeman and Fleming, 1956).

From 1952 to 1956 the average catch of cod per 100 lines fished on the shallow-water grounds fluctuated between 5000 and 6700 lb, but afterwards there was a steady decline to approximately half the catch level of the earlier years of the fishery (Fig. 2).

Differences in the weights of the deep- and shallow-water catches are clarified somewhat through an examination of the age, length, and weight distributions of cod in these catches (Fig. 4). Comparisons available for 4 years indicate much greater numbers of young, small cod in the shallow-

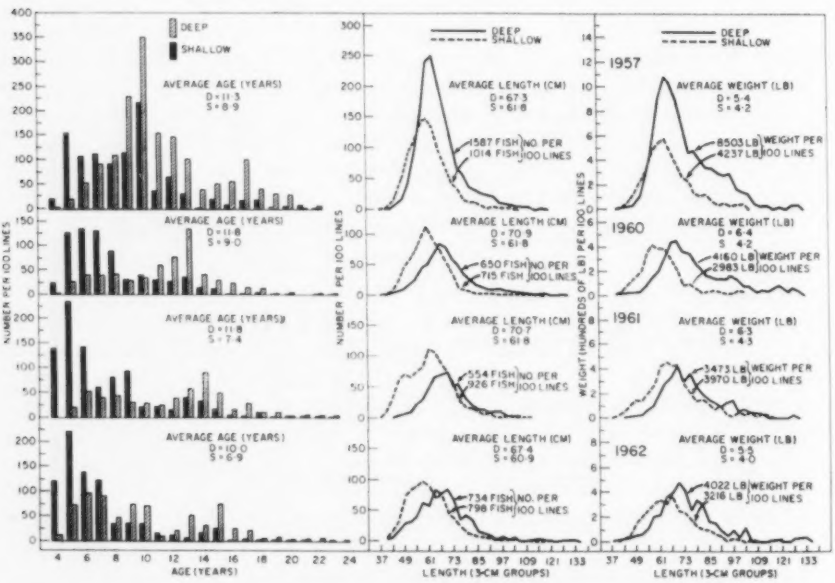


FIG. 4. Age, length, and weight distributions (per 100 lines of gear) of cod in the deep and shallow longline catches off Bonavista.

water catches, with the catch compositions being 3–4 years less in average age, 5–9 cm less in average length, and 1–2 lb less in average weight, when compared with samples from deep-water catches.

DISCUSSION AND CONCLUSIONS

In the longline fishery off Bonavista the period of consistently high catches was relatively short. There were two main reasons for this: (1) Although from 1952 to 1955 the deep-water cod stocks off Bonavista were exploited only by the local longliners, in 1956 a few European longliners and otter trawlers joined in the fishery. In 1957 much greater effort was concentrated by a larger number of large otter trawlers and longliners in the area and this has continued through the years (Templeman and Fleming, 1962). This increased exploitation resulted in a rapid reduction of the stocks. (2) To maintain a stock which is heavily exploited in this manner there would have to be reasonably constant recruitment of young fish to the stock. Samples from the longline catches revealed that there were large fluctuations in the contribution by various year-classes to the fishery, with heavy contributions coming from broods produced in the periods of 1934–35, 1939–40, 1947–48, and 1955–56, and less from the broods of intervening years. The changes which occurred in the fishery through the years are a reflection of the interaction between the decline in the older age-groups because of the intense fishery and natural death and the irregular recruitment of young fish to the fishery.

In the regular spring migration of cod to the shallow-water areas of the coast from the deep-water areas offshore the younger fish are heavily represented (Templeman and Fleming, 1956). However, as the younger fish grow older each year, larger numbers of them remain in the deep water offshore and become available to the deep-water longline fishery. Even at the present level of recruitment it is probable that a reasonably successful longline fishery could be maintained if it were exploited only by the fleet operating from Bonavista. However, it is obvious that each time a sufficiently large concentration of cod occurs in the deep water, the large otter trawlers which annually check the area will move in and reduce or disperse such concentrations before the local longline fleet can reap much benefit from them.

ACKNOWLEDGMENTS

I am grateful for the assistance of many people in the conduct of various phases of field work. Messrs D. Macfarlane and R. Molson, of the Department of Fisheries of Canada helped during 2 years in the collection of catch and effort statistics. Mr B. French and later Mr R. Russell, Managers of Bonavista Cold Storage Co. Ltd., provided facilities for field operations, and Messrs J. Abbott and T. Cuff interviewed longliner skippers on my behalf. The skippers of the longliners co-operated in giving information on their catch and effort, and permitted examination of the fish in their catches.

The following technicians of the staff of the Biological Station, St. John's, were responsible through the years for the conduct of the field work at Bonavista: Messrs W. Blackmore, W. Brown, S. Butler, T. Collier, C. Elms, L. Forward, W. Squires, and C. Woodford.

Mr T. Collier assisted in the age determinations.

REFERENCES

FRB. 1953–61. Reports of the Biological Station, St. John's. *In* Annual Report of the Fisheries Research Board of Canada, Ottawa.

TEMPLEMAN, W., AND A. M. FLEMING. 1956. The Bonavista longlining experiment, 1950–1953. *Bull. Fish. Res. Bd. Canada*, No. 109, 55 pp.

1962. Longlining experiments off the east coast of Newfoundland and southern Labrador, 1950–55. *Ibid.*, No. 141, 65 pp.

New Records and Descriptions of Plecoptera (Class Insecta)[1]

By W. E. Ricker

Fisheries Research Board of Canada
Biological Station, Nanaimo, B. C.

ABSTRACT

Descriptions are presented of the following new species: *Brachyptera fosketti, B. zelona, Capnia gregsoni, C. spenceri, C. sasquatchi, C. rogozera, C. bergi, C. cheama, C. beringi, C. sugluka, Nemoura wenatchee, Leuctra baddecka, Paraleuctra dusha, Paraperla wilsoni,* and *Chloroperla ovibovis*; and of the new subgenus *Bolshecapnia* (type *Capnia gregsoni*). Supplementary descriptions, new synonymy, or new records are given concerning *Capnia coloradensis* Claassen, *Isocapnia vedderensis* (Ricker), *Leuctra sibleyi* Claassen, *Isoperla nana* (Walsh), *Paraperla frontalis* (Banks), and six species of the *Ostrocerca* subgenus of *Nemoura*.

INTRODUCTION

The classification and distribution of animals is one of the many facets of biology that have interested Dr A. G. Huntsman during his distinguished career. In fact his first major scientific paper dealt with the distribution of holosomatous ascidians on the Pacific coast, and included descriptions of numerous new species. This paper was published by the Board of Directors of the Biological Stations of Canada in an early issue of Contributions to Canadian Biology, lineal antecedent of the present Journal of the Fisheries Research Board of Canada. Thus in an issue of this Journal which honours Dr Huntsman for his scientific contributions it is fitting that there should be one paper in the field of systematics.

The paper presented herewith concerns stoneflies, a group of freshwater organisms that are numerous enough to be of considerable importance in the biological economy of running waters. They have direct interest as food for fish, as possible predators on fish eggs and larvae, and as indicators of pollution or its absence. Knowledge of stonefly distribution and diversity in North America has many gaps, some of which are filled by the records and descriptions to follow.

Most type specimens are deposited in the Canadian National Collection of Insects (CNC) at the Entomology Research Institute, Department of Agriculture, Ottawa; or in the collection of the Illinois Natural History Survey (INHS), Urbana, Illinois. Paratypes and other material are mostly in the above collections and in the collections of Mr S. G. Jewett, Jr., of Portland, Oregon, and of the author.

Brachyptera ***fosketti*** NEW SPECIES

Male: Length of body 7–8 mm, to tips of hind wings 8.5–9.5 mm. Wings reduced: forewing 2.5 mm long, of which the outer half is bent vertically;

[1]Received for publication October 8, 1964.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

hind wing 6–7 mm long. Ninth sternite much produced, with long hairs near the tip, and lacking any ventral lobe. Anterior portion of 10th tergite with stout anteriorly-directed hairs. The epiproct (or supra-anal process) is divided into four parts (Fig. 1). The *basal bulb* is brown and is smoothly rounded or with a low dark flat-conical apex next to the groove separating it from the anterior erect member. The *anterior erect member* of the epiproct is slender, curved forward, and has low swellings laterally near the tip. The *posterior erect member* of the epiproct is separate from but frequently closely applied to the anterior; it is somewhat broader than the latter, and terminates in two hemispherical membranous bulges which are separated by an angular groove (viewed from above and a little anteriorly). On the hind surface of the posterior erect member is an opening containing a membranous *sleeve*, or posterior portion of the epiproct (Hanson, 1938); this may be almost wholly withdrawn or may be extruded to varying degrees (Fig. 2). There are two slender probe-like structures in the epiproct. The first arises from a black seed-like basal body inside the basal bulb on the right side, and is produced upward inside the anterior erect member to its top; I have never seen it protrude beyond the tip of the member, and indeed the hard sclerotization there suggests that this is impossible.[2] The second probe-like structure, here called the *filament* (Brinck, 1955), arises in the basal bulb to the left of the previous one (where it may be partly coiled but has no heavy base) and passes backward and upward to the sleeve; it may be protruded from the sleeve to varying degrees or it may be completely withdrawn (Fig. 1, 2). Upper portion of the subanal lobes strongly sclerotized, directed inward to a chisel edge; lower portion asymmetrical, mostly membranous but with oddly-shaped sclerotized portions.

FEMALE: Length of body 10–11 mm, to tip of wings 16–17 mm. Wings fully developed, lightly infuscated but without banding. There is a distinct subgenital plate whose hind margin is anterior to the hind margin of the sternite (Fig. 3); it is rounded at the sides and usually shallowly excavated medially, less often flat or slightly convex. Central part of 8th sternite marked by low sculpturing along roughly hemispherical lines; sometimes with a dark mark centrally. Ninth sternite pale medially, dark at sides; its posterior portion pale at the base, dark elsewhere, tapered evenly to a narrowly rounded or subacute tip.

Holotype ♂, allotype ♀, 31 ♂ and 25 ♀ paratypes: South Saskatchewan River at Clarksboro, Sask. (A. R. Brooks): April 10, 1949 (CNC). South Saskatchewan River at Saskatoon, Sask. (D. R. Foskett): April 13, 1939, 2 ♂, 3 ♀; December 30, 1939, 2 nymphs; (A. R. Brooks): April 14, 1940, 2 ♂, 2 ♀.

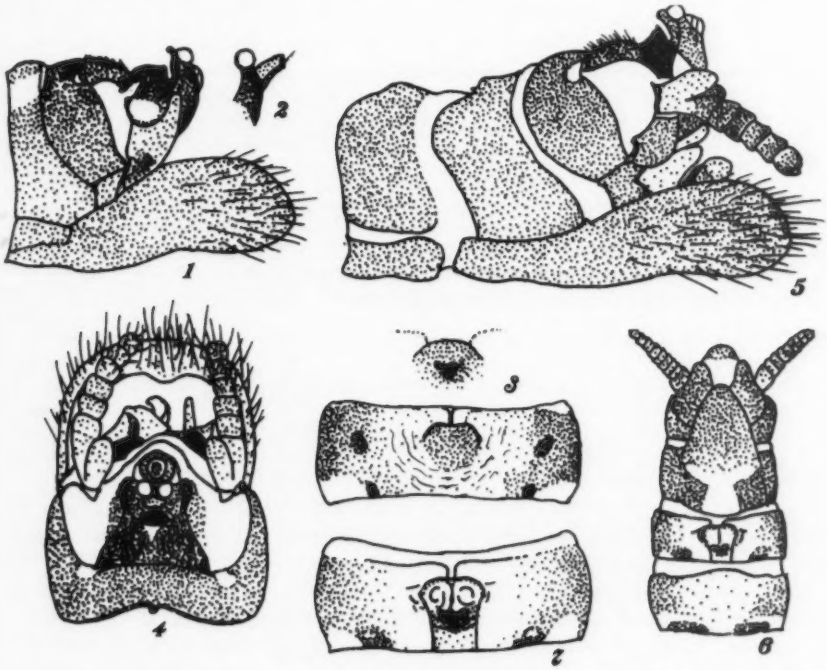
The species is named for its first collector, the versatile naturalist Dudley R. Foskett, now of Edmonton, Alberta. A comparison of *B. foskетti* with related species is given under *B. zelona*, below.

[2]Since writing the above I have seen a specimen of the closely related species *Brachyptera glacialis* in which this structure does protrude from an aperture on the anterior face immediately below the tip. This therefore should be called the *anterior filament*, while the one referred to in the next sentence becomes the *posterior filament*.

Brachyptera ***zelona*** NEW SPECIES

MALE: Length of body 9 mm, to tips of hind wings 10 mm. General colour dark brown in alcohol, black in life. In most ways very similar to *B. fosketti*. Forewing 3 mm long, including the vertically upturned outer half; hind wing 7 mm long. Tergite 10 differs from *fosketti* in having an erect conical process rather than a low knob on the basal bulb of the epiproct (Fig. 5), easily distinguished in both front and side views, but covered by the epiproct in Fig. 4.

FEMALE: Length of body 10.5–11.5 mm, to tip of wings 14.5–16 mm. Wings fully developed, lightly infuscated but without banding. There is a distinct subgenital plate whose hind margin is anterior to the hind margin of the 8th sternite (Fig. 6, 7); it is rounded at the sides and is usually shallowly excavated medially, rarely straight; light ridges running forward from the sides of the plate define a central field on the sternite. Mesal portion of the 8th sternite shallowly sculptured in an irregularly hemispherical pattern, and with a rather indefinite dark mark near the middle. Ninth sternite pale me-



Brachyptera fosketti. 1. Male abdomen, from the side; cercus removed (Clarksboro, Saskatchewan). 2. Posterior member of epiproct, with sleeve and probe partially extruded. 3. Female 8th sternite, with a second form of the subgenital plate above.

Brachyptera zelona. 4. Male abdomen, from above (Myton, Utah). 5. Male abdomen, from the side. 6. Female abdomen, from below. 7. Female 8th sternite.

dially, dark at sides; its posterior projection pale at the base, dark elsewhere, tapered evenly to a narrowly rounded or subacute tip.

Holotype ♂, allotype ♀, 2 ♀ paratypes: Myton, Utah (R. A. Z.): March 16, 1940 (INHS). Myton is situated on the Green River. Four ♀ paratypes, Green River at the town of Green River, Utah (W. E. Ricker): March 28, 1961. Other material: Central Rocky Mountain region on U.S. Highway No. 50, Colorado (W. E. Ricker): April 18, 1954, 1 ♀.

The western specimens of this group of species of *Brachyptera* have previously been recorded under the name *glacialis* Newport (Ricker, 1952), but their difference in structure now seems quite clear. The westernmost records of true *glacialis* are from Minnesota (Harden and Mickel, 1952); I have examined several from this state, and find no approach toward the structure of *fosketti* or *zelona*. On the other hand, it is possible that future collecting will demonstrate a continuous gradation of size and structure between the South Saskatchewan and Green Rivers, and that *zelona* and *fosketti* will have to be considered variants of a single species. However there is no close approach to *zelona* among the numerous male specimens of *fosketti* at hand.

The more distinctive features of the three species are included in the following key to males:

1 Posterior erect member of the epiproct very shallowly excavated posteriorly near its tip, its maximum width near the tip equal to 0.75 of the basal mound of the epiproct; anterior erect member of the epiproct produced laterally near its tip so as to be cross-shaped (front view); tip of forewing usually slightly upturned, the upturned portion not more than ¼ as long as the rest of the wing. . . . *glacialis* Newport

Posterior erect member of the epiproct angularly notched posteriorly near the tip, its maximum width near the tip about 0.5 of the basal mound; anterior erect member of the epiproct narrower than in *glacialis*, with only a slight bulge on each side near the tip; upturned portion of forewing at least half as long as the flat portion, with which it makes approximately a right angle. 2

2(1) Basal mound in front of the epiproct subconical (front view), with a black acute apex . . . . . *zelona* (new)

Basal mound in front of epiproct mostly brown and usually smoothly rounded (front view), sometimes with a low dark subacute tip. . . . . *fosketti* (new)

The females of these three species are not easily distinguished. However in *glacialis* the subgenital plate tends to be more definitely notched than in the others, and the margin laterad of the notch tends to be straighter. In *zelona* females a longitudinal line from the sides of the plate can be traced fairly clearly for the full length of the tergite.

Bolschecapnia NEW SUBGENUS

Type: *Capnia gregsoni* NEW SPECIES

This new subgenus is established for a group of species of *Capnia* Pictet from western North America, characterized by large size, presence of a ventral lobe at the base of the ♂ 8th sternite, and a ♀ subgenital plate produced well beyond the hind margin of the 8th sternite. The two structural characters

distinguish them from all other North American *Capnia* (except that the female described for *C. spinulosa* Claassen has a produced plate), while size overlap would occur only rarely. The species placed in the subgenus at the present time are *maculata* Jewett, *gregsoni* Ricker, *spenceri* Ricker, *sasquatchi* Ricker, and *rogozera* Ricker.

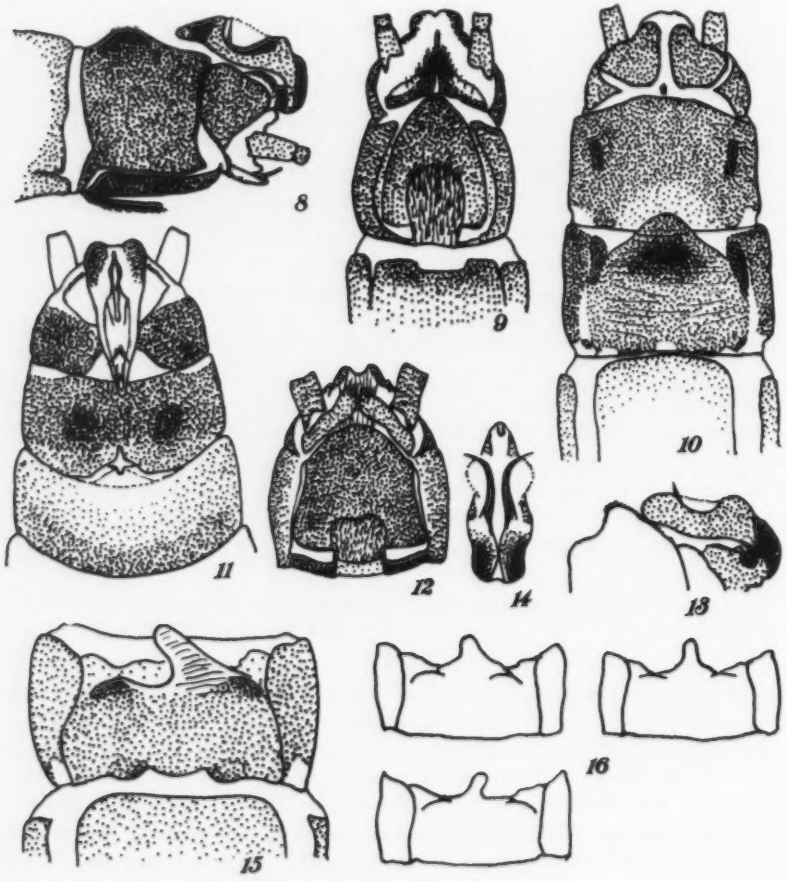
The occurrence of a lobe or vesicle at or near the base of the 9th sternite is widespread among filipalpous stoneflies and is presumably an ancestral character. It is developed in the great majority of species of Nemourinae and Leuctrinae and in many Taeniopteryginae. Among Capniinae it occurs in *Isocapnia* and *Eucapnopsis*, but is lacking from *Allocapnia*, *Paracapnia*, *Nemocapnia*, and several small European and Japanese genera. In the genus *Capnia* itself such a lobe is absent from the type species *C. nigra* Pictet and from a majority of European and Asian species. Up to recently *C. nigra* was confused with the north European *C. bifrons* Newman; this led Hanson (1946) to describe the structure of *bifrons* in detail (under the name *nigra*), and he seems to have been the first to illustrate the presence of a ventral lobe in that species. A lobe is present in a number of other old-world species, from the Caucasus to the Himalayas, but none of these approach the American *Bolshecapnia* species in details of structure of either male or female. Inclusion of these species in *Bolshecapnia* must therefore be left in abeyance; at the moment it seems undesirable. On the other hand there are two Japanese species which show considerable resemblance to *Bolshecapnia* in male and female structure, but no mention is made of a 9th-sternite ventral lobe in their descriptions: *C. bituberculata* (Uéno 1929) and *C. shirahatae* Kohno 1952. Since the ventral lobe has sometimes been omitted from descriptions, it would be desirable to re-examine these species and perhaps others; or perhaps *Bolshecapnia* should be broadened to include both lobed and lobeless species. In addition, *C. asakawana* Kohno 1952, known from the female only, has a narrow and greatly produced subgenital plate.

Capnia (*Bolshecapnia*) ***gregsoni*** NEW SPECIES

Isocapnia "species B" of Ricker (1943, p. 94, fig. 72)

MALE: Length to end of body 7–8 mm, to tip of wings 8–10 mm. Body brown in life; wings lightly infuscated, grey, somewhat reduced; venation as in the female. Abdomen sclerotized above except for the mid-line of the 1st tergite and the front portions of the mid-line of the 2nd and 3rd; hind part of the 4th to 8th tergites with somewhat weaker sclerotization than the front part. Ninth tergite darker than the more anterior ones, bearing a transverse rounded bristle-bearing prominence, or two prominences separated by a very shallow median depression (Fig. 8). Epiproct complex, with two slender curved and pointed shafts dorsally, which can be erected but normally lie mostly concealed by white membranous tissue which fills the dorsal groove in the main part of the epiproct. This tissue can be expanded into bulb-like "wings" on either side, reminiscent of the alae of conifer pollen. Sternites 2–8 fully

sclerotized, with an anterior subrectangular notch in the sclerotization. Sternite 9 darker, bearing a subrectangular basal lobe with corners broadly rounded and hind margin slightly rounded or less often straight, but not emarginate; the lobe being covered by stout golden backward-pointing bristles (Fig. 9). Subanal lobes broadly sclerotized along the mesal and front margins, with long hairs in a tuft near the tip. Fusion plate (dorsad of the lobes) slender at both ends, expanded near the middle, exceeding the length of the lobes at both ends, and attached to them by membranous connections.



Capnia gregsoni. 8. Male abdomen, from the side (Mt. Arrowsmith, Vancouver Island). 9. Male abdomen, from below. 10. Female abdomen, from below.

Capnia spenceri. 11. Male abdomen, from above (Consolation Lake, Alberta). 12. Male abdomen, from below. 13. Epiproct, from the side. 14. Epiproct, from above. 15. Female 8th sternite. 16. Three variant forms of female 8th sternite.

FEMALE: Length to end of body 8–9 mm, to tip of wings 10–11 mm. Body dark brown, wings of a light tan colour, contrasting with those of the male. Costal crossveins include the humeral, the apical, one near the cord (if Sc is considered to end in R), and sometimes one other a little proximad of the cord. Eighth sternite projected into a short rounded extension, somewhat variable in length but much broader than that of *spenceri* and always symmetrical (Fig. 10).

NYMPH: Length about 8–10 mm when mature. Body hair short; no swimming hairs on cerci. Holotype ♂, allotype ♀, 12 ♂ and 22 ♀ paratypes: Kokli Lake, between Mt. Arrowsmith and Mt. Kokli, el. about 1300 m, near Cameron Lake, Vancouver Island, British Columbia (Ferris Neave and W. E. Ricker): June 9, 1957 (CNC).

Other specimens from British Columbia: Forbidden Plateau, near Courtenay, Vancouver Island (J. D. Gregson): July 13, 1935, 2 ♀. Helen Lake, Garibaldi Park, near Squamish (J. Barton): May 12, 1951, 1 ♀. Garibaldi Park (John Ricker): May 14, 1958, 6 ♂, 2 ♀, 6 exuviae. Garibaldi Lake, Garibaldi Park (Karl Ricker): April 18, 1960, 2 ♂, 1 ♀. Head of Gwillim Creek, Valhalla Mountains, northwest of Slocan (John Ricker): July 22–31, 1958, 1 ♀.

This species is closely related to *C. spenceri*, and the location of the boundary of separation, or possibly zone of intergradation, should prove interesting. The easternmost specimen available at present, from the Valhalla range, seems indistinguishable from Coast Range specimens; while the westernmost *spenceri*, from the eastern Selkirk Mountains, are definitely of that species.

Males of the type series were collected from the snow and eroding ice at the edge of a cirque lake of about 2 hectares extent; females were partly on the snow, partly they had taken wing and were found on vegetation up to 150 m or so distant. The other collection sites also are all at or near high mountain lakes.

The species is named for its first collector, Jack Gregson, entomologist and mountaineer of Kamloops, B. C.

Capnia (*Bolshecapnia*) ***spenceri*** NEW SPECIES

MALE: Length of body 6–7 mm, to tip of wings 6 mm. Body brown, wings lightly infuscated, grey, moderately brachypterous. Tergites 1–8 as in *gregsoni*. Tergite 9 dark, with a narrow yellow hind margin at the sides, bearing a heavily sclerotized hairy hump on either side of a deep median longitudinal groove (Fig. 11). Epiproct similar to that of *gregsoni*, but somewhat thicker near the tip in side view (Fig. 13, 14). Lobe of the 9th sternite squarish, shorter and more angular than in *gregsoni*, and with the hind margin often slightly emarginate (Fig. 12).

FEMALE: Length of body 9–10 mm, to tip of wings 11–13 mm. Body brown, wings grey. Abdominal tergites 1–8 with a broad median unsclerotized stripe. Subgenital plate of sternite 8 a narrow rounded asymmetrical projection, the asymmetry being either to the right or the left, and developed in

varying degrees (Fig. 15, 16). When (rarely) almost symmetrical, the plate resembles that of *gregsoni* but is considerably narrower.

NYMPH: Length about 8–10 mm when mature. Body hair short, no swimming hairs on cerci.

Holotype ♂, allotype ♀, 33 ♂ and 15 ♀ paratypes, numerous exuviae: Consolation Lake (el. 1900 m), near Moraine Lake, Banff National Park, Alberta (W. E. Ricker): June 1, 1958 (CNC).

BRITISH COLUMBIA. Headquarters Creek, near Sorcerer Glacier, Selkirk Mtns. (John Ricker): July 14, 1960, 3 ♀. Northwest Branch of Lyell Creek, el. 1520 m, near Golden (John Ricker): June 30, 1961, 1 ♀.

The greatest structural differences between this species and *gregsoni* are the deep groove in the ♂ 9th tergite, and the narrow and usually asymmetrical ♀ subgenital plate. The asymmetry of the subgenital plate exhibited by the type series is without parallel among stoneflies of North America. Asymmetrical genital structures are known in male stoneflies, though they are exceptional, but I know of no instance where their development exhibits individual variability. Of the British Columbia specimens, two of the three from Sorcerer Glacier are quite asymmetrical, while the third and the specimen from Lyell Creek are symmetrical.

Consolation Lake was almost free of ice when the type specimens of *C. spenceri* were collected, but part of the north shore and the water nearby were covered by 3–6 m of snow from one of the spring avalanches. Specimens were found walking on the snow and hiding among rocks at the snow's edge: at noon most females were already hiding, most males still on their way. Exuviae were in depressions in the surface of the snow near a place where the water had melted the avalanche sufficiently to permit the nymphs to climb out through it.

The species is named for Dr G. J. Spencer, emeritus professor of zoology at the University of British Columbia, Vancouver, and still one of the most active entomologists in the province.

Capnia (*Bolshecapnia*) ***sasquatchi*** NEW SPECIES

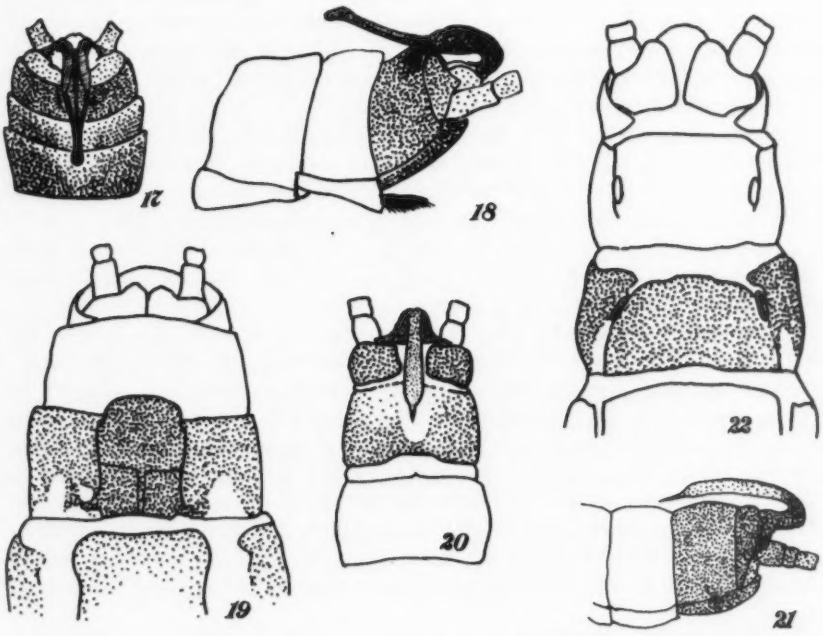
MALE: Length to end of body 6.5 mm, to tip of wings 6 mm. Wings lightly infuscated, tawny grey in the forewing; no costal crossveins proximad of the tip of the subcosta, one beyond. Ninth tergite with a low spinulous hump on either side of a broad median depression. Epiproct recurved, in dorsal view tapered and then expanded a little to a rounded tip, with median and lateral longitudinal ridges (shown black in Fig. 17) separated by a depression; in side view the epiproct is sinuous, heavier at the base (Fig. 18). Ninth sternite with an elliptical ventral lobe, one-third as long as the sternite, having a heavy coat of stout yellow spinules. Subanal lobes narrow and heavily sclerotized basally, expanded and light-coloured near the tip, which area bears numerous long white hairs; mesal margins connected by a membrane; the fusion plate above it prolonged into a narrow process.

HOLOTYPE MALE: Fraser River bridge near Agassiz, British Columbia (W. E. Ricker): February 21, 1958 (CNC).

The mild winter of 1957–58 suggested an early visit to the Fraser River to discover when the abundant *Isocapniae* would first emerge. A collection on February 21 yielded none of these, but along with numerous *Capnia elongata* and *C. columbiana* there was a lone male *Capnia*, larger and quite different from other species. The next collection, March 14, failed to produce additional specimens. It is named for the sasquatch, yeti-like forest giants of the Fraser valley Salish Indian legends.

Capnia (*Bolshecapnia*) ***rogozera*** NEW SPECIES

FEMALE: Length of body 7 mm, to tip of wings 9.5 mm. Colour dark brown in alcohol, presumably black in life. Forewings with the humeral and 2 other costal crossveins before the end of Sc in C; and one beyond. In the right forewing only there is a crossvein between R and Rs, near the junction of these veins. First anal vein expanded into the usual scar just beyond the



Capnia sasquatchi. 17. Male abdomen, from above (Agassiz, B.C.). 18. Male abdomen, from the side.

Capnia rogozera. 19. Female abdomen (Moosehorn Lake, B.C.).

Capnia bergi. 20. Male abdomen, from above (Lower Yukon River, Alaska). 21. Male abdomen, from the side. 22. Female abdomen, from below.

anal cell. Eighth sternite with a raised hairless subgenital plate definitely marked off along the whole length of the sternite, this being sclerotized only slightly more heavily than the rest of the segment. The plate is slightly narrowed near the hind margin of the sternite and is produced beyond it for a distance of about 0.18 of the length of the sternite. Under the anterior 0.4 of the subgenital plate two valves or perhaps thickenings can be seen through the transparent cuticle; they lie dorsal to the external part of the plate, and are narrowly separated from each other medially (Fig. 19).

Holotype ♀: Moosehorn Lake, British Columbia, 58°10′N, 132°07′W, el. 1370 m (R. J. Pilfrey): July 29, 1960 (CNC).

The projection of the subgenital plate suggests that this species belongs in *Bolshecapnia*, and may in fact be the female of *C. sasquatchi*.

Capnia ***bergi*** NEW SPECIES

MALE: Length of body 5–6 mm. Colour brown in alcohol, presumably black in life. Thoracic sterna typical of *Capnia* (cf. Hanson, 1946). Wings completely absent. Tergite 9 with a median oval light-coloured shallow depression; tergite 10 not sclerotized mesally. Epiproct recurved, reaching forward almost to the anterior margin of tergite 9; in dorsal view it increases gradually in width, then narrows abruptly to a slender point (Fig. 20, 21). Sternite 9 without any ventral lobe.

FEMALE: Length of body 6.5–7.5 mm. Resembles the male in the complete absence of wings. Eighth sternite somewhat recessed near the longitudinal lateral groove; the central portion of the hind margin rounded but not extending onto sternite 9, with a slight excavation on either side (Fig. 22).

Holotype ♂, allotype ♀, 2 ♂ and 11 ♀ paratypes: Pilot Station, lower Yukon River [62°0′N lat, 163°0′W long] (C. O. Berg): August 13, 1951 (Cornell University collection). Five *Capnia* nymphs are in the same sample.

Dr Berg's field notes indicate that he made a collection at this locality in a slow-flowing clear creek or slough, using a plankton net. The notes do not mention whether stoneflies were taken, but since nymphs and imagoes are present together in the collection, it is likely that this species is aquatic in the adult stage, like the wingless *Capnia* described as occurring in Lake Tahoe (Jewett, 1963). The epiproct of *bergi* resembles in general such species as *projecta* Frison and *porrecta* Jewett; the species does not resemble the two apterous *Capniae* described from Washington and Oregon by Jewett (1962).

The species is named for its collector, Dr C. O. Berg of Cornell University, whose work with sciomyzid flies may yet revolutionize the control of bilharziasis.

Capnia ***cheama*** NEW SPECIES

MALE: Length to end of body 3.5 mm, to tip of wings 3.5 mm. Colour black. Wings somewhat shortened, lacking the crossvein between C and Sc (Sc ends in R). Slanting costal (C–R) crossvein at the cord. No lobe at base

of 9th sternite. Tergite 8 with a median dark-pigmented and hairy process on the hind margin, shallowly excavated at the tip and somewhat overhanging tergite 9 (Fig. 24). Tergites 9 and 10 unsclerotized in a broad median field. Epiproct directed anteriorly; it has a broad basal support, posterior rounded projection, slender stalk, broad middle portion which is declivitous anteriorly, and a terminal blade that is axe-like in side view, slender in dorsal view (Fig. 23).

FEMALE: Length to end of body 4 mm, to tip of wings 5.5 mm. Wings fully developed, C–Sc crossvein present near the cord, slanting C–R crossvein beyond the cord. Eighth sternite with extra sclerotization along the margin, which is recessed at the sides, excavated at the middle, and is not produced over sternite 9 (Fig. 25).

Holotype ♂, allotype ♀, 2 ♂ and 1 ♀ paratype: Fraser River bridge near Agassiz, British Columbia (W. E. Ricker): March 14, 1958 (CNC). Other paratypes from the same locality: May 1, 1957, 1 ♀; March 26, 1960, 9 ♂, 7 ♀.

YUKON. Rampart House [on the Porcupine River, 67°N lat, 141°W long] (C. C. Loan): April 30, 1951, 1 ♂, 1 ♀ (CNC).

One of the smallest stoneflies, this species has an epiproct somewhat akin to *californica* Claassen, *excavata* Claassen, *teresa* Claassen, and *tumida* Claassen, but it is not really close to any of these. It is named for Mt. Cheam, a well-known landmark near the type locality.

Capnia ***beringi*** NEW SPECIES

MALE: Length of body 4.5–5 mm, to tip of wings 6–7 mm. Colour black in life; wings lightly and evenly infuscated. Tergites lacking humps. Epiproct fully recurved forward, bent near the middle, ending on the 8th segment (Fig. 26). The epiproct is medium stout, swollen near the middle (in the dorsal and side views), its tip narrow, spine-like, slightly decurved (Fig. 27). No ventral lobe on 9th sternite.

FEMALE: Length of body 5.5–6.5 mm, to tip of wings 7–8 mm. Seventh sternite slightly produced and rounded. Eighth sternite with hind margin (subgenital plate) somewhat recessed and having a small light-coloured "insert" medially; the anterior middle portion forming a rather vague light triangle (Fig. 28).

Holotype ♂, allotype ♀: Summit Lake, British Columbia, el. 1280 m, at mile 392 on Alaska Highway (E. E. MacDougall): July 17, 1959 (CNC). All Summit Lake specimens listed below are paratypes.

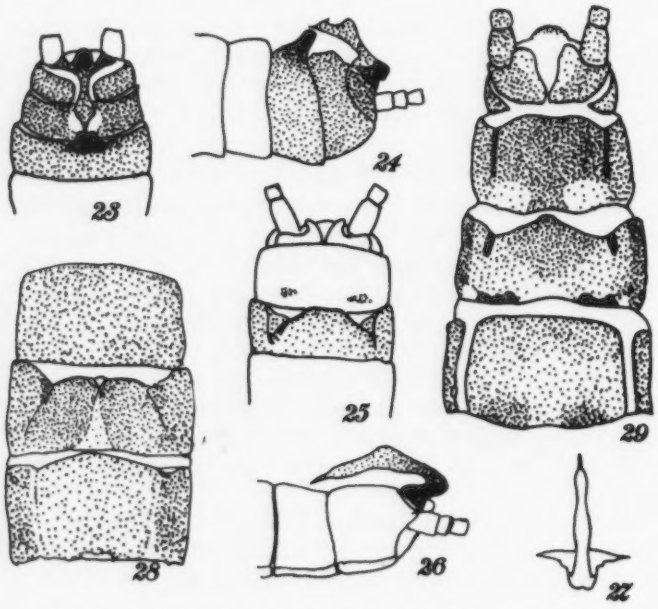
ALASKA. Paxon Lodge, Gulkana, el. 1220 m (W. R. M. Mason): August 8, 1951, 1 ♂, 10 ♀. Cape Thompson (R. Madge): July 23, 1961 4 ♂, 3 ♀. Umiat (R. Madge): July 30, 1959, 7 ♂, 13 ♀.

BRITISH COLUMBIA. Summit Lake (E. E. MacDougall and R. E. Leech): July 16, 1959, 6 ♂, 9 ♀; July 17, 1959, 7 ♂, 24 ♀; July 30, 1959, 4 ♀; August 19, 1959, 8 ♂, 21 ♀; August 21, 1959, 2 ♀; "August" 1959, 1 ♂, 5 ♀.

This species is rather close to *Capnia oenone* Neave 1929, but the latter has the epiproct more slender, less bent, and with less swelling at the middle. The distribution of *beringi* from the Bering Sea coast to a little south of the Yukon boundary suggests that it survived the ice ages in the unglaciated Yukon Valley, whereas *oenone* more probably lived south of the Continental ice sheet. The known distributions do not overlap, though *oenone* has been taken as far north as Pete Lake, B. C. (57°56′N, 131°56′W).

Capnia sugluka NEW SPECIES

FEMALE: Length of body 5–6.5 mm; to tip of wings 4–6 mm. A small *Capnia*, brown in alcohol, presumably black in life. Wings shortened, but venation typical of *Capnia*. Cerci with 19 segments. Eighth sternite with narrow irregular dark sclerotization laterally at the front margin; hind margin produced into a blunt subtriangular subgenital plate, slightly excavated on either side near the tip, and fairly deeply excavated near the sides of the sternite, where a narrow dark band runs forward a short distance (Fig. 29). Ninth sternite slightly produced and shallowly emarginate, with elongate longitu-



Capnia cheama. 23. Male abdomen, from above (Agassiz, B.C.). 24. Male abdomen, from the side. 25. Female abdomen, from below.

Capnia beringi. 26. Male abdomen, from the side (Summit Lake, B.C.). 27. Epiproct, from above. 28. Female abdomen, from below.

Capnia sugluka. 29. Tip of female abdomen, from below (Payne Bay, Quebec).

dinal dark bands at either side, and sclerotization reduced anteriorly at either side.

Holotype ♀ and 43 ♀ paratypes: Payne Bay, west side of Ungava Bay, Quebec (W. Mason): July 14, 1958 (CNC). Other paratypes from same locality, collector, and year: July 8, 15 ♀; July 20, 22 ♀; July 21, 6 ♀; July 25, 5 ♀; July 27, 2 ♀; July 30, 2 ♀; August 11, 3 ♀; August 18, 9 ♀. Other material: Sugluk, Quebec (H. Huckel): August 1954, 1 ♀ (CNC).

A new *Capnia* from the shores of Ungava Bay and Hudson Strait was an unexpected product of the Northern Insect Survey's operations during the 1950s. The absence of males is frustrating; they will be tiny and probably almost wingless. The 8th sternite of this species differs considerably from the two others known from northern Quebec (*C. vernalis*, *C. manitoba*), and it is much smaller than *C. labradora* from the Newfoundland Labrador. West of Hudson Bay and on Baffin Island *C. nearctica* is common, but *sugluka* is a much smaller species, while its 8th sternite is more produced, less "set off" at the side, and lacks a wrinkled hind portion with glistening-black sclerotization. *Capnia sugluka* most resembles *C. vidua* of Europe, as far as female structure is concerned. This parallels the situation with *C. nearctica*, whose closest relative is the European *C. atra*.

Capnia coloradensis Claassen 1937a

MALE: Study of the type by the late Dr T. H. Frison and myself, plus comparison with new material, shows that Claassens' figure 8 represents a relaxed specimen in which the posterior unsclerotized portion of the 8th tergite is fully stretched out; unfortunately he shows this portion as heavily sclerotized. Figure 30 here is of a similarly extended specimen; more usually the segments are partly telescoped so that the process of the 8th tergite appears at or close to the posterior margin of the tergite, rather than close to its middle. The 7th tergite is modified in all specimens by having a narrow heavily-sclerotized curved band on the anterior margin, and a median shining area behind it. The shining area is usually flat and light in colour (Fig. 31), but some of the specimens from the Yukon have a dark knob rising from it, of sizes varying from barely perceptible to the extreme shown in Fig. 30. No such knob is suggested in the holotype or in any of the Montana specimens. Tergites 2–6 in all specimens have a narrow dark band along the anterior margin, but this is interrupted medially. There is no ventral lobe on the 9th sternite. Male specimens from the Yukon seem to have the epiproct somewhat thicker and more curved, in side view, than those from Colorado and Montana, but the difference is very slight.

FEMALE: Sternite 7 moderately sclerotized, appearing swollen in side view and bearing many long stout pale hairs on its posterior half; the sclerotization is continuous, across the intersegmental groove, with the mostly darker sclerotization of the shining 8th sternite, which bears fewer and shorter hairs. In the intersegmental groove there are two narrow lateral prongs of harder sclerotization. Hind margin of the 8th sternite rounded, tending to be flat

at the tip, but rather variable in contour. The pigmentation of the 8th sternite may be solid or may have obscure irregular patterns due to structures lying below (Fig. 32).

MONTANA (R. A. Hays). Hyalite Creek, Gallatin Co.: April 4, 1951, 1 ♂; March 14, 1952, 1 ♂. Lower part of Deep Creek, 13 miles from Townsend, Broadwater Co.: March 7, 1954, 2 ♀. Upper part of Deep Creek, 21 miles from Townsend, Broadwater Co.: March 7, 1954, 17 ♂, 14 ♀.

YUKON. Dickson Lake, Mt. Mye, el. 1520 m, 62°21'N, 133°8'W (J. E. H. Martin): June 14, 1960, 1 ♀. North Fork Pass, Ogilvie Mtns., el. 1250–1310 m (R. E. Leech and P. J. Skitsko): June 12, 1962, 11 ♂, 12 ♀; June 13, 4 ♂, 6 ♀; June 17, 3 ♂, 25 ♀; June 19, 2 ♀.

The female associated with *coloradensis* by Claassen (1937a, figure 5) belongs to the *columbiana* group of species.

Isocapnia vedderensis (Ricker 1943) — NEW COMBINATION

When Hanson's (1946) study of capniid external morphology became available, it was apparent that the thoracic structure of the species *vedderensis* had greater resemblance to *Isocapnia* than to the genus *Eucapnopsis* in which it was described. It now seems time to place *vedderensis* in *Isocapnia* because it differs no more from the type species *grandis* Banks than do several other species currently assigned to *Isocapnia* (Ricker, 1959). These species present considerable diversity in sternal structure (along with a general similarity); and it happens that the mesofurcasternal arms (Hanson's terminology), which are bound to the sides of the postfurcasternum in *grandis*, are free from the postfurcasternum in all other species of the genus, including *vedderensis*. It is of course possible that a general review of capniid nomenclature would suggest that *Isocapnia* would best be considered a subgenus of *Eucapnopsis*. The records below have accumulated since the original description:

ALBERTA (W. E. Ricker). Spray River, Banff: June 5, 1957, 1 ♀. Tributaries of Bow Lake and River, Banff National Park: May 30, 1958, 2 ♂.

BRITISH COLUMBIA (W. E. Ricker). Fraser River near Agassiz (1957): April 17, 3 ♂, 1 ♀; April 24, 3 ♂, 3 ♀; May 1, 1 ♀. Chilliwack River at Vedder Crossing, March 26, 1960, 1 ♀.

MONTANA (R. A. Hays, 1951). Spanish Creek, Highway 191 Bridge, Gallatin Co.: May 6, 2 ♂, 2 ♀. Hyalite Creek, Gallatin Co.: May 17, 1 ♀.

UTAH. Near the summit south of Indian Canyon (Knowlton and Wood): April 23, 1943, 4 ♂, 1 ♀.

SUBGENUS *Ostrocerca* Ricker 1952

The males of this subgenus of *Nemoura* are so interesting, complex and distinctive that they may have prevented adequate attention being given to the females. At any rate most existing descriptions and illustrations of females are inadequate or misleading. At this time I am able to describe the previously unknown female of *truncata*, figure three others, present a new key, and list some new records for all six species. Unfortunately the female I tentatively assigned to *complexa* Claassen in 1952 has still not been definitely associated

with male *complexa*, although some additional specimens are now available. The key to females given below replaces that of Ricker (1952, p. 39).

1 7th sternite lacking sclerotization, its hind margin not produced; margin of 8th sternite somewhat produced and broadly and almost rectangularly excavated (eastern) ..... *truncata* Claassen

7th sternite somewhat sclerotized along its hind margin, at least near the middle (this inconspicuous in *albidipennis*); 8th sternite not as above 2

2(1) Hind margin of 7th sternite swollen into three smooth humps, the middle one larger than the lateral ones; margin of 8th sternite broadly and smoothly excavated (western) ..... *foersteri* Ricker

Hind margin of the 7th sternite not as above 3

3(2) 7th sternite produced over most of the eighth, its hind margin broadly rounded (eastern) ..... *prolongata* Claassen

7th sternite less produced (usually little produced), terminating in a distinct nipple (best seen in side view) 4

4(3) 7th sternite triangularly produced medially to fill a notch in the front margin of the 8th, its tip terminating in a rather large sclerotized nipple; margin of 8th sternite triangularly produced, deeply and narrowly notched (western) ..... *dimicki* Frison

Front margin of the 8th sternite almost straight, with the nipple of the 7th sternite produced over it for a short distance; 8th sternite straight, or produced and shallowly excavated (eastern) 5

5(4) Nipple of the 7th sternite parallel-sided, prominent; hind margin of 8th sternite straight, with a little extra sclerotization at the mid-line ..... ? *complexa* Claassen

Nipple of the 7th sternite blunt-conical, weak, very easily overlooked in ventral view; hind margin of 8th very broadly notched or excavated, without extra sclerotization near the middle ..... *albidipennis* Walker

Nemoura (*Ostrocerca*) *albidipennis* Walker 1852

In the description and figure of the female type of this species by Ricker (1938, p. 133) the nipple on the 7th sternite was omitted. Figure 33 shows this feature, which is almost sure to be overlooked unless a specimen is examined in side view.

N. albidipennis seems to be the commonest eastern *Ostrocerca*. The following records are additional to Walker's type and to the records given by Needham and Claassen (1925) and Sprules (1947) under the name *N. serrata* Claassen.

NEW HAMPSHIRE (Frison and Ross). Warren: June 21, 1941, 1 ♂. Small stream at cog railway, Mt. Washington: June 22, 1941, 1 ♀.

NEW YORK. Old Forge: July, 1905, 1 ♀. Rock City, Cattaraugus Co.: June 6, 1915, 1 ♀.

ONTARIO. Peterson Creek, Algonquin Park (B. V. Peterson): May 24, 1960, 4 ♂, 1 ♀, 2 nymphs. Papineau Creek and Spring Creek, Maynooth (J. F. McAlpine): June 19–22, 1953, 5 ♂, 19 ♀. Meridian Road, Forest Station, Petawawa (J. R. Vockeroth): May 28, 1959, 2 ♂, 1 ♀.

QUEBEC. Harrington Lake, Gatineau Park (H. J. Huckel): May 27, 1954, 1 ♂, 6 ♀; (E. E. Sterns): May 30, 1954, 3 ♂, 3 ♀. McDonald Creek near Meach Lake, Gatineau Park (W. E. Ricker): May 23, 1964, 1 ♂, 5 ♀; May 31, 1964, 2 ♂, 6 ♀. Fortune Creek, Gatineau Park (W. E. Ricker): May 23, 1964, 1 ♂, 2 ♀. Masham Mills, Stations C and D (F. P. Ide): May 25, 1935, 1 ♀; June 5, 1935, 1 ♀. Temiskaming (F. P. Ide): June 22, 1939, 1 ♀. Lindsay's Creek, Wakefield (J. L. McDunnough): May 31, 1930, 1 ♀.

Nemoura complexa Claassen 1937b (?)

A female has been assigned tentatively to this species, and figured (Ricker, 1952). Collection records for females of this type are as follows:

NEW YORK. Death Creek near Raquette Lake, Adirondack Park (Frison and Ross): June 19, 1941, 1 ♀.

ONTARIO (B. V. Peterson). Small stream east of Lake of Two Rivers, Algonquin Park, May 25, 1960, 1 ♀. Lake of Two Rivers Nature Trail, Algonquin Park, May 25, 1960, 1 ♀.

QUEBEC. Covey Hill (C. H. Curran): June 17, 1924, 2 ♀ (CNC) Mountain north of Glen Sutton, el. 500 m (W. E. Ricker): July 12, 1964, 2 ♀.

Nemoura (*Ostrocerca*) *dimicki* Frison 1936

The female of this species has been figured by Frison (1936, p. 265); and it was also illustrated by Needham and Claassen (1925, p. 361, figure 19) as the female of *N. californica*. Both figures show a median projection on the 8th sternite situated well behind its front margin. In fact, this projection is the nipple of the 7th sternite, of which a sclerotized central area extends far back and covers a triangular notch in the front margin of the 8th (Fig. 34). The notch of the 8th sternite of this species varies in width: Figure 34 is intermediate between the two forms illustrated by the authors above. Some records additional to those of Frison (1936), Hoppe (1938), and Ricker (1943) are as follows:

BRITISH COLUMBIA. Bowser (R. Coyles): May 30 to June 18, 1955, 1 ♂, 1 ♀. Langford: March 12, 1959, 1 ♂; April 2, 1959, 1 ♂; April 20, 1959, 1 ♂ (CNC). Mt. Bruce, el. 250 m, Saltspring Island (W. E. Ricker): April 4, 1956, 1♀.

WASHINGTON. Whites: March 28, 1931, many ♂ ♀; April 2, 1931, 5 ♂, 4 ♀.

Nemoura (*Ostrocerca*) *foersteri* Ricker 1943

Figure 40 of Ricker (1943) fails to show the three humps of the sclerotized hind margin of the female 7th sternite, and the hind margin of the 8th sternite is more angular than usual; a typical specimen is shown in Fig. 35. In addition to the type series from mainland British Columbia, this species has been recorded from the Willamette valley of Oregon by Jewett.

BRITISH COLUMBIA (Vancouver Island). Bowser (R. Coyles): May 28, 1955, 1 ♂. Qualicum Bay (G. E. Shewell): June 15, 1955, 1 ♂, 11 ♀. Moss Lake, Englewood (H. A. Magel): June 14, 1952, 1 ♀.

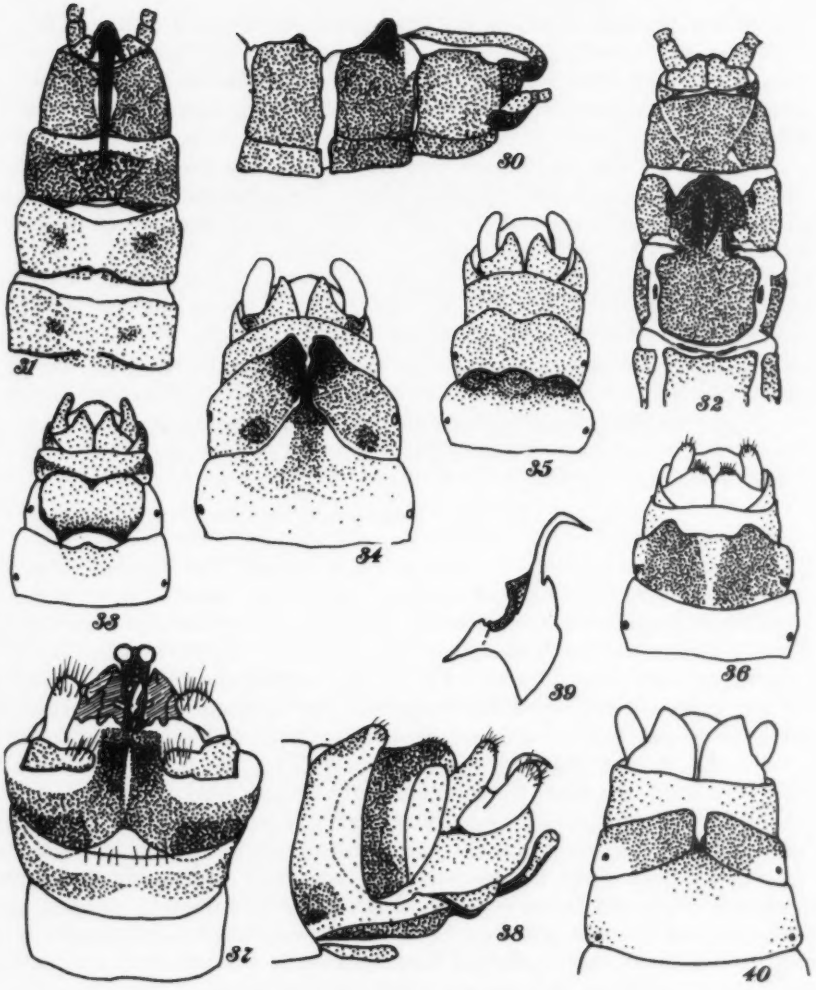
Nemoura (*Ostrocerca*) *prolongata* Claassen 1923

The first Canadian record is as follows.

NEW BRUNSWICK. Fredericton (N. R. Brown): June 5, 1947, 1 ♂.

Nemoura (*Ostrocerca*) *truncata* Claassen 1923

FEMALE: Length of body 5–5.5 mm, to tip of wings 8.5–9 mm. Colour black with grey unbanded wings. Eighth sternite more heavily sclerotized



Capnia coloradensis. 30. Male abdomen of a specimen having an extreme hump on the 7th tergite, from the side (North Fork Pass, Yukon). 31. Male abdomen of a specimen lacking a hump on the 7th tergite, from above (North Fork Pass, Yukon). 32. Female abdomen, from below (Deep Creek, Montana).

Nemoura albidipennis. 33. Tip of female abdomen, from below (Maynooth, Ontario).

Nemoura dimicki. 34. Tip of female abdomen, from below (Cultus Lake, B.C.).

Nemoura foersteri. 35. Tip of female abdomen, from below (Cultus Lake, B.C.).

Nemoura truncata. 36. Tip of female abdomen, from below (Gatineau Park, Quebec).

Nemoura wenatchee. 37. Male abdomen, from above (Lake Wenatchee, Washington). 38. Male abdomen, from the side. 39. Right subanal lobe of male, from below. 40. Female abdomen, from below.

than 9 and 10, produced over the 9th by a distance equal to 0.5 of its own lateral length; broadly and rather deeply notched, with the bottom of the notch almost straight to gently sinuate (Fig. 36). Seventh sternite lacking sclerotization (except at the spiracles), and lacking any posterior median projection.

This species has been known only from two males, the type from Massachusetts and one from Ohio (Ricker, 1952). The following records extend its known range southward and northward, and indicate that it can be locally abundant.

MARYLAND. Near Yellow Springs, Frederick Co. (E.L. Mockford): May 7, 1955, 2 ♂, 1 ♀.

NEW YORK. West Danby (W. T. Davis): May 30, 1915, 1 ♀.

ONTARIO. Small stream east of Lake of Two Rivers, Algonquin Park (R. V. Peterson): May 25, 1960, 1 ♀.

QUEBEC. McDonald Creek, near Meach Lake, Gatineau Park (W. E. Ricker): May 10, 1964, 32 ♂, 10 ♀; May 23, 1964, 1 ♂, 2 ♀; May 31, 1964, 1 ♂, 6 ♀; June 20, 1964, 1 ♂.

Nemoura (*Malenka*) ***wenatchee*** NEW SPECIES

MALE: Length of body 5.5 mm, to tip of wings 8 mm. Colour brown to black above, with yellowish areas on the back of the head, fore part of the mesothorax, and sides of the pronotum; below mostly yellow with broad brown areas on the sides of the meso- and metasternum; legs yellow, antennae brown; wings completely infuscated with light brown, slightly darker along the cord. General structure and venation typical of the subgenus *Malenka* (Ricker, 1952). Mesobasal lobes of cerci rounded, very hairy on the tip, sclerotized on the anterior surface, membranous posteriorly (Fig. 37). Cerci broad at the base, narrowing to a blunt tip curved slightly inward; membranous. Posterior part of the 10th tergite bent downward, heavily pigmented but with a narrow light median stripe; the epiproct recurved to a nearly erect position at the tip; broader than thick; its tip somewhat excavated, with rounded lobes on either side (Fig. 38). Subanal lobes ascending, surrounding the epiproct and meeting above it; each divided into a very short blunt inner branch and a long slender outer branch that is bent backwards at right angles near the tip (Fig. 39). Tip of the 9th sternite acute, its basal lobe (vesicle) slender.

FEMALE: Length of body 6.5 mm, to tip of wings 8 mm. Eighth sternite produced over $\frac{1}{3}$ of the 9th; its cleft is a broad notch distally, while proximally it is a narrow slit bordered by extra sclerotization (Fig. 40). Seventh sternite produced halfway over the 8th, broadly rounded and swollen, lacking any distinct nipple, though a shallow groove separates the swollen portion from the anterior margin of the segment (side view).

Holotype ♂, allotype ♀. Small spring creek ("Skabbage Creek") at Glacier View Forest Camp, south side of Lake Wenatchee, Washington (W. E. Ricker): April 27, 1963. Paratypes: same locality and date, 12 ♂, 1 ♀; same locality, May 19, 1961, 1 ♂, 2 ♀.

This species is one of the largest of the subgenus *Malenka*. In the key (Ricker, 1952, p. 30) the male will run to couplet 3, where the subanal lobe will distinguish it (divided into 1 short prong and 1 very long prong). The female runs to *cornuta*, from which species it is distinguished by larger size, and by the absence of irregularities on the margin of the notch of the 8th sternite.

Leuctra ***baddecka*** NEW SPECIES

FEMALE: Length of body 6.5–8 mm; to tip of wings 8.5–10 mm. Colour brown in alcohol, presumably black in life. Abdominal tergites 1–8 with a sclerotized median stripe, separated on each side from the sclerotized portion of the pleurites by an unsclerotized area about twice as broad as the median stripe. Tergite 10 fully sclerotized, 9 almost so. Sternites 1–9 sclerotized medially, membranous laterally, the width of the membranous area decreasing rearward. Eighth sternite produced about $\frac{1}{3}$, notched medially, each side emarginate near the notch and tufted with strong hairs laterally (Fig. 41). Ninth sternite as long as the tergite; sclerotized except for a small median posterior spot.

Holotype ♀ and 4 ♀ paratypes: Baddeck Forks, Nova Scotia (J. McDunnough): July 2, 1936 (CNC).

No known female of *Leuctra* s.s. has the dorsal abdominal stripe — a feature found in *Paraleuctra*. However this species lacks other characteristics of female *Paraleuctra*, such as the shortened 9th sternite, the slender cerci, and the more distal position of the M–Cu crossvein. For the moment *baddecka* is described as a *Leuctra*, but the male will be needed to confirm its true relationships.

Leuctra (s.s.) *sibleyi* Claassen 1923

Claassen's description and figures illustrate this large species as having a strong bilobed "border" pattern on the 7th tergite, seemingly no less definite than that of the 8th. Study of the type and other material indicates that the 7th tergite pattern, if present, is variable in outline, and is always much less distinct than that of the 8th. Frequently the 7th tergite is fully sclerotized and lacks any pattern except for the four dark muscle scars; fairly often the anteromesal area is more lightly pigmented than the rest (Fig. 42). The pattern on the 8th tergite is invariably well developed.

In life *L. sibleyi* is conspicuous among *Leuctrae* for its large size and for the yellow colour distributed as follows: head between ocelli and compound eyes, sides of mesonotum, proximal half to two-thirds of femora (except a narrow dorsal dark stripe on the proximal third), proximal tenth of the fore wings, most of prosternum, broad mesal portions of meso- and metasterna and also a narrow lateral stripe on each, under side of coxae and trochanters, sterna 1–7 and anterior half of 8.

Occasional specimens of *Leuctra biloba* Claassen have an 8th-tergite pattern fairly close to some specimens of *sibleyi*. As well as being a smaller species,

biloba has the lobe of the 9th sternite near the middle of the sternite, whereas in *sibleyi* it is near the anterior margin.

Claassen reported *L. sibleyi* only from the neighbourhood of Ithaca, New York, and Sprules (1947) collected it in Algonquin Park near Whitney, Ontario. The records below indicate a wide distribution for the species in eastern North America, penetrating to the middle west in cool spring streams.

ILLINOIS. Bell Smith Spring, Pope Co. (Bouseman and Mockford): May 2, 1959, 1 ♂.

INDIANA. Armstrong Branch at Speed Hollow, Springville, Lawrence Co. (Burks, Ricker, Ross, and Scott): April 26, 1946, 1 ♂, 1 ♀. Leonard Springs, Bloomington, Monroe Co. (Burks, Ricker, Ross, and Scott): April 25, 1946, 2 ♂, 2 ♀. Blair Springs, Monroe Co. (D. C. Scott): April 6, 1947, 2 ♂, 1 ♀.

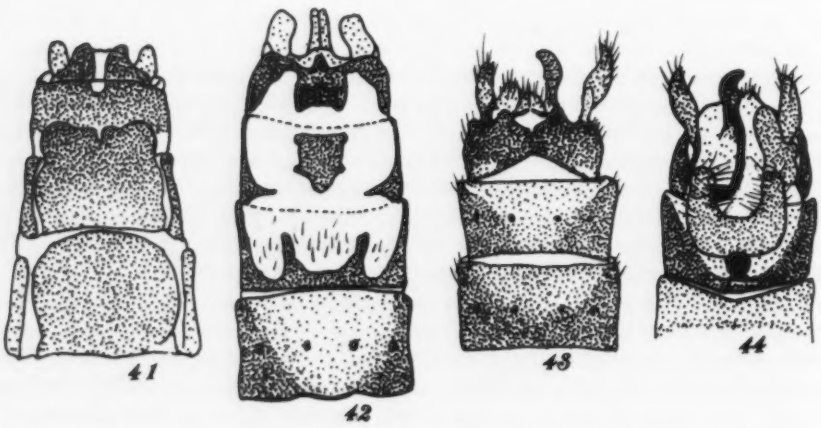
MARYLAND. Yellow Springs, Frederick Co. (E. L. Mockford): May 7, 1955, 1 ♂, 1 ♀.

MASSACHUSETTS. Petersham (Milne and Greene): July 5, 1935, 1 ♂.

NEW YORK. Adirondack Lodge (P. W. Claassen): July 1, 1923, 1 ♂, 2 ♀. Artists Brook, Essex Co. (J. C. Bradley): June 28, 1923, 5 ♂. Cranberry Lake: June 26, 1920, 1 ♂. Inlet Brook, McLean: May 27, 1924, 1 ♂. Penn Yan on Keuka Lake: May 30, 1923, 2 ♂. Slaterville: May 10, 1925, 2 ♂.

NORTH CAROLINA. Small stream 2 miles south of Newfound Gap, Great Smoky Mountains National Park (D. C. Scott): April 14, 1949, 1 ♂, 3 ♀. Smokemount Campground, GSMNP (D. C. Scott): May 16, 1949, 1 ♂.

QUEBEC. Covey Hill (C. H. Curran): June 17, 1924, 1 ♂, 4 ♀; (G. S. Walley): June 15, 1927, 1 ♂. Masham Mills, Sta. X. (G. E. Boucher): July 2, 1935, 1 ♂; (F. P. Ide): June 19, 1936, 1 ♂. Fortune Creek at Ridge Road parking lot, Gatineau Park (W. E. Ricker): May 10, 1964, 1 ♂, 23 ♀; May 23, 1 ♀; May 31, 1 ♀; June 20, 2 ♂, 1 ♀; June 28, 3 ♂, 1 ♀.



Leuctra baddecka. 41. Female abdomen, from below (Baddeck Forks, N.S.).

Leuctra sibleyi. 42. Male abdomen, from above (Gatineau Park, Quebec).

Paraleuctra dusha. 43. Male abdomen, from above (Barkerville, B.C.). 44. Male abdomen, from below.

TENNESSEE. West Prong of Pigeon River at Park Headquarters, GSMNP (W. E. Ricker): April 21, 1949, 7 ♂, 3 ♀.

VIRGINIA. Lydia (Ross and Burks): April 20, 1938, 1 ♂, 3 ♀.

Paraleuctra ***dusha*** NEW SPECIES

MALE: Length of body 6 mm; to tips of wings, 8 mm. Colour brown in alcohol, possibly black in life. Posterior plate of the 9th sternite deeply cleft behind, with long inwardly-directed hairs on either arm. Subanal lobes asymmetrical (Fig. 44): the left one broad, slightly tapered, with a lateral projection and rounded at the tip; the right one slender, bent inward then backward, heavily sclerotized ventrally, its tip expanded, grey, hairless, and delicately sculptured — somewhat as in *occidentalis* Banks (= *bradleyi* Claassen). Ventral lobe of the 9th sternite slightly behind the front margin; covered with stout backwardly-directed hairs. Cerci long, sclerotized, flattened on the mesal surface, somewhat curved mesad and with long hairs near the tip, which bears a short subacute projection; the right cercus also with an inner angle at the base. Epiproct a swollen rounded lobe bearing long hairs and a somewhat shorter slender spine at the tip. Tenth tergite bilobed on the hind margin, scalloped at the side, bearing two curved sclerotized bars beneath (Fig. 43). Ninth and 8th tergites with lighter sclerotization posteriorly.

Holotype ♂: Barkerville, British Columbia (E. R. Buckell): June 29, 1949 (CNC).

This specimen, remarkable for its asymmetry, clearly belongs in *Paraleuctra*. The deeply-notched 9th sternite resembles *P. occidentalis*, as does the left subanal lobe to some extent (though it is much longer and more curved in *occidentalis*). Different from this and from all other species of the genus are the bulbous (not hook-shaped) epiproct, the absence of strong spines on the cerci, and of course the asymmetry of the subanal lobes. The latter feature might suggest that this is an abnormal specimen, that the right lobe should "really" resemble the left. Even more speculative is the possibility that this may be a gynandromorphic specimen of *P. occidentalis* in which varying degrees of intermediacy between male and female structure are exhibited by the epiproct, the cerci, and the subanal lobes (the left lobe far more than the right, of course). It seems far more likely, however, that the specimen represents an undescribed species, even if its asymmetry is abnormal; in any event a name for it will be useful.

The name *dusha* (= spirit) refers obliquely to the type locality, which was briefly the largest settlement in British Columbia, later becoming a ghost town; and perhaps also to this species, which may prove to be substantial.

Isoperla nana (Walsh 1862)

1862. *Chloroperla nana* Walsh, 1862, p. 367. Type locality: Rock Island, Illinois.
1907. *Alloperla nana* Banks, 1907, p. 13.
1940. *Alloperla nana* Claassen, 1940, p. 187.
1900. *Chloroperla minuta* Banks, 1900, p. 244. **New synonymy.**
1906. *Alloperla minuta* Banks 1906, p. 175.

1907. *Alloperla minuta* Banks 1907, p. 13.
1925. *Isoperla minuta* Needham and Claassen, 1925, p. 147.
1935. *Isoperla minuta* Frison, 1935, pp. 433, 453.

Walsh's description of *nana* is as follows:

"*Chloroperla nana*, n. sp. — Differs from the above in size, in the head being immaculate above and below, and in the prothorax being one-half wider than long, its angles rounded, and with a broad, median, luteous vitta. The hyaline streaks on the wings are absent.

Length to tip of wings 6½ mill. Alar expanse 11½ mill. Abd. 2 mill. One ♀ ? specimen."

"The above" in this description refers to *Chloroperla brunneipennis* Walsh (= *Perlesta placida* Hagen), a species that Walsh regarded as allied to *C. nana* probably because both have a conspicuously yellow costa.

In 1935 and again in 1942 Dr Frison expressed his opinion that the type of *nana* Walsh was probably the same as *I. minuta* (Banks). It now seems time to make this association definite. The diagnostic part of Walsh's description is the combination of small size and striped pronotum. (A luteous vitta is a deep-orange stripe, according to the Shorter Oxford; however Walsh frequently uses the term luteous for parts of stoneflies which are orange-yellow or yellow.) This combination can apply only to *I. minuta*, among described stoneflies, and the intensive collecting done in Illinois and adjacent States makes the existence of an undescribed one in that region most unlikely. Other parts of Walsh's description also agree with *minuta*, but two points require comment: 1. "Head immaculate" does not describe most *minuta*, which usually have a yellow spot in the ocellar triangle. However the size of the spot varies; it is frequently inconspicuous and occasionally absent. 2. Frison (1935, p. 433) points out that *I. minuta* "does not have the hyaline streaks on the wings entirely absent, as stated in the original description [of *C. nana*]." To clarify this I quote Walsh's description of the wings of *Chloroperla brunneipennis*:

"Wings all brownish, costa yellowish; veins the colour of the wing; front wings with a streak between the post-median and postcostal veins, and the region of the origin of the accessory subcostal, hyaline."

This hyaline or clear streak is very easily seen in *Perlesta placida* [= *brunneipennis* above], a species which in life often has dark brown or almost black wings; it lies in the fold of the wing between Cu_2 and A_1. In *I. minuta* the wing membrane is less heavily coloured, so that this streak is always much less easy to see, and is practically indistinguishable in a teneral specimen; thus Walsh may easily have overlooked it.

In summary, there is no important discrepancy between Walsh's description of *C. nana* and the species currently called *I. minuta*, while the distinctive points are such as to preclude its being any other known species.

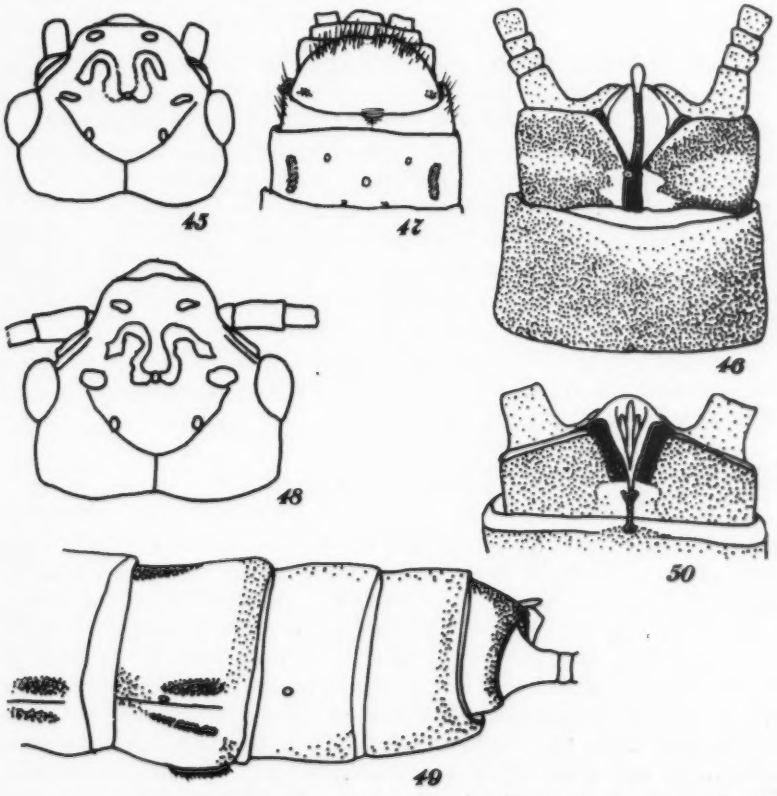
Paraperla ***wilsoni*** NEW SPECIES

1943. *Paraperla frontalis* Ricker (in part — not Banks, 1902). Four specimens listed as *frontalis* in this 1943 paper prove to be *wilsoni* — in the list below these are the holotype, allotype, and the first two specimens listed under "other material."

MALE: Length of body 13–14 mm; to tip of wings 13–15 mm. Colour, venation, and most details of structure as in *P. frontalis* Banks. Head capsule not so long and less angular behind the eyes than in *frontalis* (compare Fig. 45 and 48). Wings as long as abdomen or up to 2 mm longer. Epiproct mostly sclerotized, except near the tip; tip straight or nearly so, never bent 90°; stylets absent; paragenital plates narrower than in *frontalis*, their posteromesal corners broadly rounded (Fig. 46).

FEMALE: Length of body 14–16 mm, to tip of wings 15–18 mm. Subgenital plate shallowly and roundly notched (Fig. 47), or scarcely notched at all.

Holotype ♂: Chiliwack River at Vedder Crossing, British Columbia, May 10–26, 1937 (W. E. Ricker). Allotype ♀: the same, April 25, 1937 (Stanley Spencer). Both are in the CNC. Other material as follows:



Paraperla wilsoni. 45. Head of male holotype (Vedder Crossing, B.C.). 46. Male abdomen, from above—relaxed, cowl opened (Summit Lake, B.C.). 47. Female abdomen, from below (Vedder Crossing, B.C.).

Paraperla frontalis. 48. Head of male (Nanaimo, B.C.). 49. Male abdomen, from the side (Minerva, Colorado). 50. Male abdomen, from above — not relaxed, cowl covering most of the epiproct (Minerva, Colo.).

BRITISH COLUMBIA. Sweltzer Creek, Cultus Lake (Stanley Spencer): March 12, 1941, 1 ♀. Liumchin Lake outlet, el. 1070 m, near Cultus Lake (W. E. Ricker): June 27, 1937, 1 ♀. Barkerville (E. R. Buckell): June 29, 1948, 1 ♀. Mt. Revelstoke (G. R. Holland): July 10, 1952, 1 ♂. Glacier (R. H. Mann): June 18, 1946, 1 ♀. Atlin, el. 1200 m (H. Huckel): August 22, 1935, 1 ♀. Summit Lake, mile 392 on Alaska Hwy., el. 1300 m (E. E. MacDougall and R. E. Leech 1959): June 25, 1 ♂, 1 ♀; June 26, 1 ♀; July 5, 1 ♀; July 27, 1 ♀.

CALIFORNIA. Creek at 2600 m elevation, 1 mile east of summit of Tioga Pass, Yosemite National Park (W. E. Ricker): June 21, 1950, 1 ♂.

OREGON. Wallowa Lake (S. G. Jewett, Jr.): May 31, 1960, ♂ ♀.

WASHINGTON. Fryingpan Creek, el. 1400 m, NE side of Mt. Rainier (W. E. Ricker): July 23, 1937, 1 ♀.

YUKON. Vangorda Creek, 62°18′N, 133°15′W, el. 1170 m (J. E. H. Martin): 1 ♂, 1 ♀. North Fork Crossing, Mile 42 on Aklavik Road, Ogilvie Mtns., el. 1070 m (R. E. Leech): July 6, 1962, 2 ♀.

Paraperla wilsoni differs from *P. frontalis* in: smaller size; less angular hind corners of the head; male epiproct more sclerotized and always straight or nearly so at the tip; absence of lateral stylets; and a smaller notch in the female subgenital plate. *Paraperla frontalis* specimens from the western cordilleran ranges (Oregon and northward) and the Canadian Rockies differ from *wilsoni* also in having the tip of the epiproct bent downward.

The available specimens of *wilsoni* tend to come from more northern localities than most *frontalis* and, in a given locality, from greater elevations. The two type specimens, however, are from near sea-level, and from a stream where *frontalis* was collected much more frequently than *wilsoni*.

The species is named for Mr Carl Wilson of Vedder Crossing, B.C., whose home overlooks the type locality, and who was my companion on a number of local expeditions during the middle 1930s.

Paraperla frontalis Banks 1902

Geographical variation in this species is apparent in the form of the tip of the epiproct. The type (from Beulah, New Mexico) has never been illustrated. Figures 49 and 50 are from a specimen in nearby Colorado at Minerva: the tip of the epiproct is practically straight in this specimen, and is nearly so in a male from Blairsden, California. A slightly decurved tip is found in specimens from Hyalite Creek in southern Montana, while one from extreme southern Alberta is somewhat more curved. The typical form of the Coast and Cascade Ranges, from British Columbia to Oregon, has the tip of the epiproct slender and bent 90°; this is illustrated in Needham and Claassen's (1925) plate 23, figure 4, which shows the epiproct and stylets in the erect position. The female subgenital plate varies less consistently, but specimens with a broad shallow notch forming a sharp angle medially are common on the coast, while a deeper notch that is rounded medially is commoner inland (especially the Hyalite Creek specimens).

There has been some confusion of *wilsoni* with *frontalis* (Ricker, 1943, and possibly elsewhere); a list of specimens I have recently determined as *frontalis* is as follows:

ALBERTA. Carthew Lake, Waterton Lakes National Park (D. S. Rawson): July 22, 1937, 1 ♂, 1 ♀.

BRITISH COLUMBIA — mainland. Salmo (G. J. Spencer): May 12, 1947, 1 ♀. Chilliwack River at Vedder Crossing (W. E. Ricker): May 9 to June 14, 1937, 8 ♂, 5 ♀. Sweltzer Creek, Cultus Lake (W. E. Ricker): April 4, 1933, 1 ♀; May 5, 1937, 1 ♀. Harrison River at Chehalis Indian Reserve (W. E. Ricker): April 17, 1957, 1 ♂. Summit Lake, mile 392 on Alaska Hwy. (R. E. Leech): June 26, 1959, 1 ♀. Gold Creek, 14 miles E. of Terrace (B. S. Heming): June 17, 1960, 1 ♂.

BRITISH COLUMBIA — Vancouver Island (W. E. Ricker). Cameron Creek near Cameron Lake, June 19, 1955, 4 ♂, 6 ♀. Cameron Creek at 520 m elevation, June 28, 1952, 1 ♀. Haslam Creek near Nanaimo, April 12 to May 23, 1952–57, numerous ♂ ♀.

CALIFORNIA. Tributary of Smith Creek, el. 1500 m, Blairsden (W. E. Ricker): June 11, 1952, 1 ♂, 1 ♀.

COLORADO. Minerva, el. 3050 m (H. H. and J. A. Ross): June 14, 1954, 1 ♂.

MONTANA. Hyalite Creek, Gallatin Co. (R. A. Hays): June 21, 1951, 4 ♂, 4 ♀.

NEW MEXICO. Panchuela, near Cowles: July 9, 1944, 1 ♀.

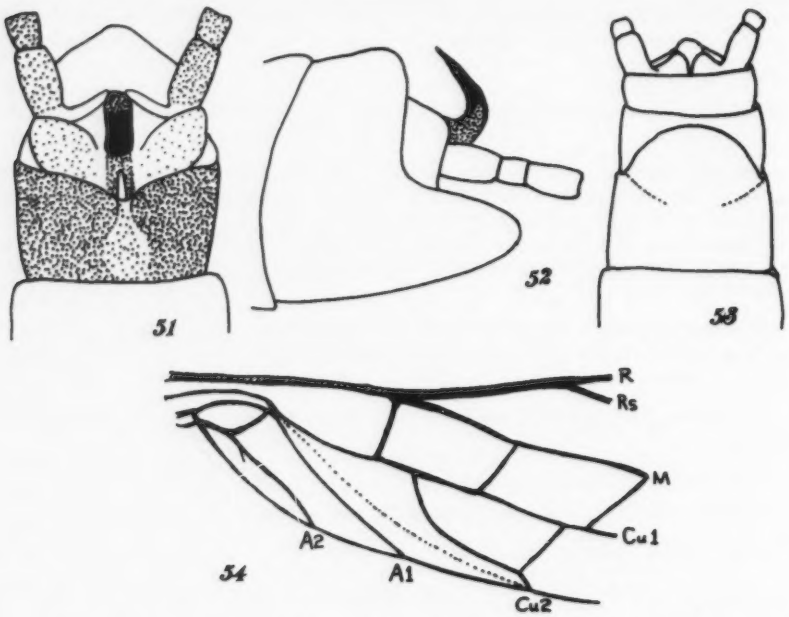
OREGON. Metolius River (K. M. Fender): January 18, 1947, 1 ♀. Oak Creek, Corvallis (E. E. Ball): April 13, 1934, 1 ♂.

WASHINGTON. Snoqualmie (G. Hoppe): May 5, 1932, 1 ♂, 1 ♀. Cedar River, Maple Valley (G. Hoppe): April 18, 1931, 2 ♂; May 14, 1932, 1 ♂.

YUKON. Dawson (W. W. Judd): June 15, 1949, 2 ♂. North Fork Crossing, mile 42 on Aklavik Road, Ogilvie Mtns. (P. J. Skitsko): July 3, 1962, 1 ♀.

Chloroperla (s.s.) ***ovibovis*** NEW SPECIES

MALE: Length of body 5.5 mm, to tip of wings 8 mm. General colour yellow with darker markings. Head yellow at sides and in front, light brown in ocellar region, darker behind. Pronotum brown on all the margins, the mid-line and the rugosites, with a narrow black line down the mid-line and in a good deal of both the anterior and the posterior submarginal grooves; otherwise yellow. Meso- and metanotum with a black U-mark posteriorly, containing a median stripe a little longer than the arms of the U. Abdomen yellow with a dark median stripe on tergites 1–8, and lateral stripes on 1–3. Antennae, legs, and cerci brown. Wings clear, venation mostly as in European species of *Chloroperla*. The second anal vein of the fore wing has a very short branch (Fig. 54); this is presumably a remnant of the A_3 of *Alloperla*, etc. Three anal veins in hind wing: A_1 is as long as Cu_2 and lies close to it; A_2 is somewhat shorter; A_3 is about a third as long as A_1. Ninth tergite pale medially, the hind margin with long dense hairs on either side of a hairless median notch. Epiproct with its basal portion lying in a groove of the 10th tergite, its free portion recurved and strongly sclerotized and pigmented, the tip being thin



Chloroperla ovibovis. 51. Male abdomen, from above (Muskox Lake, Mackenzie). 52. Male abdomen, from the side. 53. Female abdomen, from below. 54. Venation of posterior basal portion of right forewing of allotype.

wedge-shaped (Fig. 51, 52). Eighth sternite lacking any terminal lobe. Ninth sternite much produced and slightly upturned. In ventral view, sclerotized bands can be seen on the aedeagus lying dorsal to the 9th sternite.

FEMALE: Length of body 6 mm; to tip of wings 9 mm. Similar to the male except for the terminalia. Subgenital plate (8th sternite) produced over $\frac{2}{3}$ of 9th sternite, broadly rounded (Fig. 53).

Holotype ♂, allotype ♀; Muskox Lake, Back River drainage, Mackenzie [64.5°N lat, 108°W long] (J. G. Chillcott): July 20, 1953 (CNC). Paratype ♀: same locality and collector, August 5, 1953.

This species differs from the only other American *Chloroperla*, *C. terna* Frison, in the less reduced anal variation of the hind wing. It is close to such European species as *Chloroperla burmeisteri* Pictet. The stub of A_2 is, however, a feature not described from Eurasian species. The male genitalia ally this species closely to the subgenus *Triznaka* of *Alloperla*, particularly *A. diversa*.

REFERENCES

BANKS, NATHAN. 1900. New genera and species of nearctic neuropteroid insects. *Trans. Amer. Ent. Soc.*, **26**: 239–259.

1902. Notes and descriptions of Perlidae. *Canadian Ent.*, **34**: 123–125.

1906. On the perlid genus *Chloroperla*. *Ent. News*, **17**: 174–175.

1907. Catalogue of the neuropteroid insects (except Odonata) of the United States. American Entomological Society, Philadelphia, 53 pp.

BRINCK, PER. 1955. Reproductive systems and mating in Plecoptera. *Opuscula Entomologica*, **21**: 57–127.

CLAASSEN, P. W. 1923. New species of North American Plecoptera. *Canadian Ent.*, **55**: 257–263, 281–292.
1937a. New species of stoneflies (Plecoptera). *Ibid.*, **69**: 79–82.
1937b. New species of stoneflies (Plecoptera). *J. Kansas Ent. Soc.*, **10**: 42–51.
1940. A catalog of the Plecoptera of the world. *Cornell Univ. Agr. Exp. Sta., Memoir* No. 232, 235 pp.

FRISON, T. H. 1935. The stoneflies, or Plecoptera, of Illinois. *Bull. Illinois Nat. Hist. Surv.* 20, pp. 281–471.
1936. Some new species of stoneflies from Oregon (Plecoptera). *Ann. Ent. Soc. Amer.*, **29**: 256–265.
1942. Studies of North American Plecoptera, with special reference to the fauna of Illinois. *Bull. Illinois Nat. Hist. Surv.*, *22*, pp. 231–355.

HANSON, J. F. 1938. Studies on the Plecoptera of North America, I. *Bull. Brooklyn Ent. Soc.*, **23**(2): 79–83.
1946. Comparative morphology and taxonomy of the Capniidae (Plecoptera). *Amer. Midland Naturalist*, **35**(1): 193–249.

HARDEN, P. H., AND C. E. MICKEL. 1952. The stoneflies of Minnesota (Plecoptera). *Univ. Minnesota Agr. Exp. Sta., Tech. Bull.* No. 201, 84 pp.

HOPPE, GERTRUDE N. 1938. Plecoptera of Washington. *Univ. Washington Publ. Biol.*, **4**(2): 139–174.

JEWETT, S. G. 1962. New stoneflies and records from the Pacific coast of the United States. *Pan-Pacific Ent.*, **38**(1): 15–20.
1963. A stonefly aquatic in the adult stage. *Science*, **139**: 484–485.

KOHNO, M. 1952. Notes on Japanese Capniidae with descriptions of new species (Plecoptera). *Mushi*, **23**(2): 17–28.

NEAVE, FERRIS. 1929. Report of the Jasper Park lakes investigations. II. Plecoptera. *Contr. Canadian Biol. Fish.*, **4**: 159–168.

NEEDHAM, J. G., AND P. W. CLAASSEN. 1925. A monograph of the Plecoptera or stoneflies of America north of Mexico. *Thos. Say Foundation of the Entomol. Soc. Amer., Publ.* No. 2, pp. 1–397.

RICKER, W. E. 1938. Notes on specimens of American Plecoptera in European collections. *Trans. Royal Canadian Inst.*, **22**(1): 129–156.
1943. Stoneflies of southwestern British Columbia. *Indiana Univ. Publ., Sci. Ser.* No. 12, 145 pp.
1952. Systematic studies in Plecoptera. *Ibid.*, No. 18, 200 pp.
1959. The species of *Isocapnia* Banks (Insecta, Plecoptera, Nemouridae). *Canadian J. Zool.*, **37**: 639–653.

SPRULES, W. M. 1947. An ecological investigation of stream insects in Algonquin Park, Ontario. *Univ. Toronto Studies, Biol. Ser.* No. 56, 81 pp. (*Publ. Ontario Fish. Res. Lab.*, No. 69).

UÉNO, M. 1929. Studies on the stoneflies of Japan. *Memoirs Coll. Sci. Kyoto Imp. Univ.*, B, **4**(2): 97–155.

WALKER, FRANCIS. 1852. Catalogue of the specimens of neuropterous insects in the British Museum, Part I. London.

WALSH, B. D. 1863. List of the Pseudoneuroptera of Illinois, etc. *Proc. Acad. Nat. Sci. Philadelphia* for 1862, pp. 363–367.

Effect of DDT on Temperature Selection by Young Atlantic Salmon, *Salmo salar*[1,2]

By D. M. Ogilvie[3] and J. M. Anderson[4]

ABSTRACT

Exposure of Atlantic salmon underyearlings for 24 hr to sublethal doses of DDT, ranging from 5 to 50 ppb, resulted in changes in the selected temperature. Low doses produced a downwards shift in the selected temperature whereas higher doses produced an upwards shift. The DDT effect appeared to be more marked for warm-acclimated fish (17°C) than for cold-acclimated ones (8°C). In addition exposure of warm-acclimated fish to 10 ppb DDT or more appeared to make them extremely sensitive to cold water and there was some evidence to suggest that the lower lethal limit may have been raised. It is suggested that DDT may interfere with the normal thermal acclimation mechanism.

INTRODUCTION

Of the several physiological mechanisms in fish which tend to prevent the deleterious effects of temperature extremes, perhaps the most striking are behavioural ones. For example goldfish in a uniformly warm environment will lower the temperature by a conditioned response to a lever which, when depressed, produces a jet of cold water (Rozin and Mayer, 1961). The best known, however, is the tendency of fish, when placed in a suitable gradient of temperature, to be found most frequently within a relatively narrow range of the temperatures available to them. The response can be described quantitatively as that temperature range where the frequency of occurrence is greatest when observations are made periodically over a reasonable length of time. The term given this modal value is usually the "selected temperature." Less frequently the selected temperature is defined on the basis of the mean (Brett, 1952), or a certain pre-determined percentage (Mantleman, 1958) of the frequency distributions.

The selected temperature is a labile characteristic whose value has been shown to depend not only upon the species, but also upon acclimation temperature (Fry, 1947; Pitt *et al.*, 1956; Ferguson, 1958) and season (Sullivan, 1953; Mantleman, 1958). Light does not appear to change the absolute value of the selected temperature in fish, but usually there is an inverse relationship between the intensity of light and the precision of selection (Sullivan and Fisher, 1954; Ferguson, 1958).

The possibility that pre-exposure to DDT might also affect temperature responses of fish was first suggested from observations made in New Brunswick in 1960 (F.R.B. Annual Report, 1960–61, p. 65). Surviving salmon taken

[1]Received for publication December 9, 1964.

[2]Department of Biology, University of New Brunswick, Fredericton, New Brunswick. Based on a thesis submitted by the senior author in partial fulfilment of the requirements for the degree of Master of Science, University of New Brunswick.

[3]Present address: Department of Zoology, University of Western Ontario, London, Ontario.

[4]Present address: Department of Biology, Carleton University, Ottawa, Ontario.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

from rivers that had been sprayed with DDT were shown in laboratory work to be inordinately sensitive to low temperatures, as evidenced by a high mortality rate when exposed to water at 1–5°C.

This paper describes the effect on the selected temperature of young Atlantic salmon (*Salmo salar* L.) following exposure to sublethal doses of DDT (1,1,1-trichloro-2,2-bis (*p*-chlorophenyl) ethane). Some of the results have a bearing on the DDT-induced delayed mortality referred to above.

EXPERIMENTAL

Organisms

Atlantic salmon underyearlings, 5–10 cm in length and 2–6 g in weight, were obtained at periodic intervals from a local hatchery and were held at the University in plastic or stainless-steel tanks supplied continually with city water which had been sand- and charcoal-filtered. Pipes leading from city mains were of plastic composition. Fish were fed daily on ground beef liver.

Fish were exposed to DDT (*p,p'* isomer approximately 77%) for 24 hr immediately prior to an experiment, in initial concentrations ranging from 5 to 50 parts per billion by weight (ppb). No mortality occurred at any of these concentrations. In other experiments, where salmon of similar size were exposed for 24 hr to DDT which resulted in some mortality (i.e. >50 ppb DDT), the survivors, when transferred to clean running water, were still living several months afterwards when observations were discontinued. There is good evidence therefore, that although the fish were destroyed at the end of each of the experiments reported here, the DDT treatments were truly sublethal.

Apparatus

Exposure to DDT was done in glass battery jars to which had been added sufficient DDT dissolved in 1 ml of acetone and 10 litres of water to give the desired initial concentration. Ten fish were added to each battery jar.

The temperature gradient was established in a trough 3 inches wide by $1\frac{5}{8}$ inches deep and 76 inches long, cut in a cylindrical aluminum bar 5 inches in diameter. The surfaces of the metal in the longitudinal channel were coated with a grey-coloured plastic paint. One 500-w electrothermal heating tape ran the full length of the bar, strapped to its undersurface. Two other 250-w tapes ran from the designated warm end to the middle of the bar. Each heating element was connected to a variable voltage supply by which the amount of heat supplied to the bar could be regulated. The assembly was well heat-lagged with asbestos. Aerated water, previously cooled to about 2°C by passing it through aluminum coils in a refrigerated bath, flowed slowly (20 litres/hr) into the designated cold end of the trough and was gradually warmed as it flowed along the trough. The water was drained at the opposite (warm) end by a constant-level siphon contained in a $2\frac{1}{2}$-inch long compartment separated from the rest of the trough by a plastic screen. Water level in the trough was maintained at $\frac{3}{4}$ inch.

To facilitate recording position of fish in the gradient, the trough was marked off into 21 'compartments' each $3\frac{1}{2}$ inches long. Temperatures were measured by six stainless-steel thermistor probes evenly spaced along the trough (in the mid-point of compartments 1, 5, 9, 13, 17, and 21). The above arrangement provided an approximately linear temperature gradient which in these experiments varied from about 3°C to 28°C.

The experiments were performed in a darkroom with uniform, dim light supplied through a sheet of frosted plexiglass which ran the length of the trough 3 ft above it. The fish were viewed from above, but at a distance from the apparatus, by the aid of a mirror attached at an angle to the light box.

Procedure

After the temperature gradient was established, the fish, usually 10 in number, were introduced into the trough. After an initial exploratory behaviour lasting about 5 min, the fish settled down to a routine swimming behaviour. Nonetheless, observations were not begun until the fish had been in the apparatus for 1 hr. Position of fish with respect to the 21 compartments was noted every minute for 1 hr. In order to facilitate rapid and accurate recording of the location of the 10 fish, the observer used a tape recorder from which the required information was later extracted. Temperature readings were taken approximately every 8 min to check the gradient which in practice showed little or no variation throughout the course of each experiment. The mean temperature of each compartment was determined (by interpolation where necessary) and the location of the fish at each observation translated into temperature. From the information thus accumulated it was then possible to determine the frequency with which the fish were found at different temperatures. The selected temperature is the temperature range corresponding to the mode of the frequency distribution plot.

In February of 1962, preliminary single experiments were done involving pretreatment of fish (10 in each case) to 10, 30, and 50 ppb DDT. Acclimation temperature was 8°C but the temperature during the exposure to DDT was 10°C. The remaining experiments were done in June and July of 1963. The fish were taken from the general holding tanks (at about 14°C) and put into special acclimation tanks at 17 ± 0.5°C for at least 2 weeks before being used in an experiment. The temperature during DDT exposure was the same as the acclimation temperature. Five experiments each were done on control fish and on fish exposed to DDT concentrations of 5, 30, and 50 ppb. Four experiments were done using 10 ppb DDT and a single experiment each was done with 20 and 40 ppb DDT. A total then of 210 treated fish and 50 control fish was used.

RESULTS

At a constant temperature (15°C) and flowing water, the distribution was clearly bimodal (Fig. 1). Animals were found at the ends of the trough, in about equal numbers, far more frequently than at intervening locations.

Neither end of the trough had any shadows. The end-peaks, therefore, probably represent a thigmotactic response of the fish to the corners and end surfaces. When still water was used, results similar to those in Fig. 1 were obtained, from which it is concluded the distribution of the fish is not influenced by the slow movement *per se* of the water.

Figure 2 shows the distribution of control fish (top panel), acclimated to 8°C, in the presence of a thermal gradient. The bimodal distribution which characterized the non-gradient situation has been replaced by a unimodal one with the fish selecting the temperature range 5–7°C. The remaining histograms show the results of the preliminary experiments (8°C acclimation) involving pretreatment of fish to various concentrations of DDT. The 10 ppb DDT fish selected 3–5°C, which is *below* the control value, whereas the selected temperatures of the 30 ppb and 50 ppb DDT fish were 9–11°C and 11–13°C, respectively, both of which are *above* the control value.

In the more extensive series of experiments (17°C acclimation), pre-exposure to DDT in all cases, except that for 5 ppb DDT, resulted in a rightwards, i.e. warmwards, shift in the frequency distribution of the fish in the trough (Fig. 3). The shift towards the colder temperatures, previously suggested in Fig. 2, is also seen in Fig. 3 but here for 5 ppb DDT rather than 10 ppb DDT. This coldwards shift is clearly not a marked one in either case. Its significance has been tested statistically. In view of the skewness of the frequency distributions, the chi-squared test was used. The results for the controls and the 5 ppb DDT-treated fish (Fig. 3) were arranged in a 2×2 contingency table in which the distribution of the fish up to the 5–7°C interval (the selected

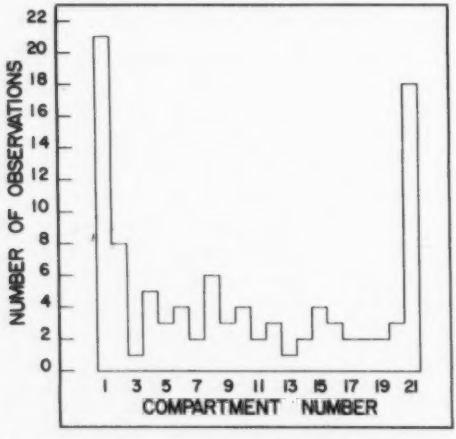


FIG. 1. Frequency with which untreated young Atlantic salmon were observed at different positions in the temperature selection trough which was filled with flowing water at a uniform temperature (15°C). Similar results were obtained when the apparatus was filled with still water at a uniform temperature.

temperature for the DDT-treated fish) was compared with the distribution at temperatures beyond this range. The probability that the calculated value of χ^2 (5.78) would occur by chance alone was $<.05$, $>.01$. It appears then that the lowering of the selected temperature by low concentrations of DDT is real as well as apparent.

It will also be noted from Fig. 3 that some of the distributions, notably those for 10 and 30 ppb DDT treatments, indicate considerable imprecision with regard to selected temperature. This results from variation between various replications and is probably the consequence of variability between experiments in the amount of DDT freely suspended in the water and thus potentially able to affect the fish. The difficulty arises from the variation in the amount of DDT adsorbed onto the glass walls of the exposure aquaria, and

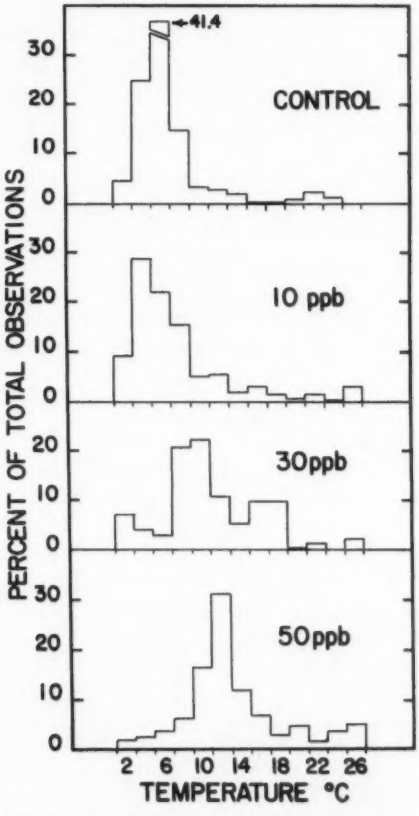


FIG. 2. Frequency with which untreated fish, and fish exposed to 10, 30, and 50 ppb DDT, were observed at the various temperatures in the gradient trough. Acclimation was at 8°C; exposure to DDT at 10°C.

onto the fish detritus. Holden (1962) estimated that such adsorption ranged from 36 to 51% of the DDT added in his studies on the uptake of DDT by brown trout.

In order to see more clearly the trends suggested in Fig. 2 and 3, the selected temperatures, taken as the mid-point of the modal value for the frequency distributions, have been plotted against DDT concentration (Fig. 4). The curves describing these results (8°C-acclimated fish, lower line, 17°C-acclimated fish, upper line) have been drawn by visual inspection.

For the warm-acclimated fish there appears to be a gradation in the response to DDT which reaches a maximum at about 40 ppb. This maximum represents about an 8°C increase in the selected temperature. In general, the same situation prevails for the cold-acclimated fish, although there is a suggestion that DDT in excess of 50 ppb is required to produce a maximum effect.

All of the values for the cold-acclimated fish lie below those for the warm-acclimated ones (Fig. 4). In the case of the control fish this is to be expected on the basis of the usual relationship found between acclimation temperature and selected temperature. The 2°C shift for control fish is not, however, large. A similar small lability for selected temperature has been shown for several species of Pacific salmon (Brett, 1952).

Also of some interest was a curious behavioural response that was frequently observed when DDT-treated fish encountered temperatures of about

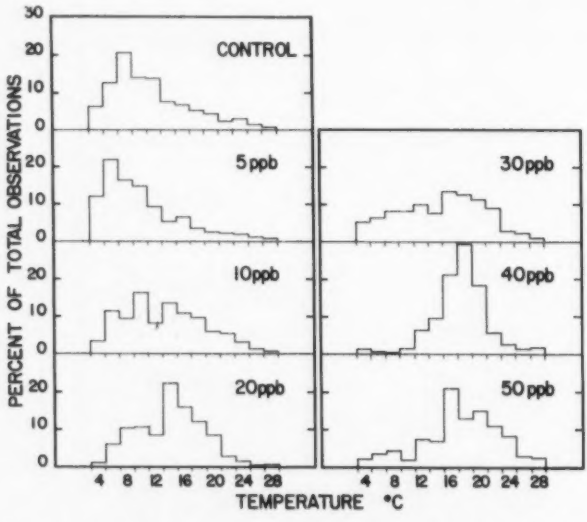


FIG. 3. Frequency with which untreated and DDT-exposed salmon were observed at the various gradient temperatures. The controls and 5, 30, and 50 ppb DDT represent the pooled results of five separate experiments each. Four experiments were done at 10 ppb DDT, and one each at 20 and 40 ppb DDT. Both acclimation and DDT exposure were at 17°C.

3.5°C or less. Typically this occurred when a fish, swimming in the direction of the affluent end of the gradient, reached the cold water, whereupon it would suddenly become hyperactive, exhibiting what can best be described as an "avoidance response." Usually the fish would swim rapidly out of the cold water into the warmer regions of the trough. If, as occasionally happened, the "cold response" failed to take the animal immediately out of the cold end, the fish would as a rule lose its equilibrium and swim feebly upside down. Death followed on the two or three occasions when the experimenter did not intervene. Normally a fish exhibiting these symptoms was gently nudged with a glass rod back up the gradient. Upon reaching warmer water the animal invariably regained its equilibrium quickly, its behaviour becoming indistinguishable from that of the rest of the fish. The response to the cold was, therefore, reversible. This response was only seen for the 17°C-acclimated fish and then only for those concentrations of DDT greater than 5 ppb. The severity of the symptoms, and frequency of occurrence, of the cold response appeared to vary directly with DDT concentration. The response was not seen in control fish even when they encountered water just above 0°C.

DISCUSSION

The selected temperatures of our untreated fish were below their respective acclimation temperature, particularly so in the case of the 17°C acclimation experiments (8°C selected temperature). These results are at odds with what one might expect on the basis that "In general the preferred temperature is considerably higher than the acclimation temperature at low thermal acclimations, but this difference decreases up to the final preferendum, where both coincide" (Ferguson, 1958). They also are at odds with the work of Fisher

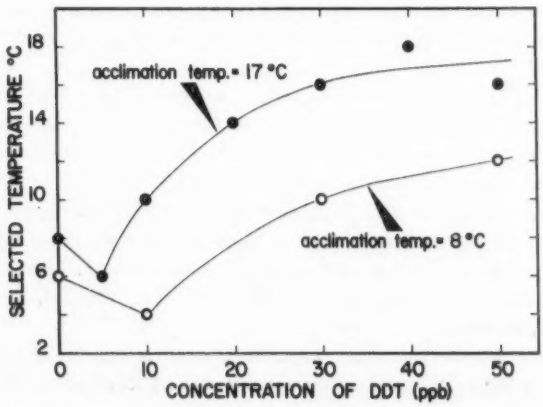


FIG. 4. The relationship between selected temperature, taken as the mid-point of the temperature interval for the modal value of the frequency distribution, and DDT exposure. 17°C-acclimated fish, upper points: 8°C-acclimated fish, lower points. (Data taken from Fig. 3 and 4.)

and Elson (1950), who found that the selected temperature of Atlantic salmon acclimated to about 14°C was 14°C, and with Mantleman (1958) who claims that Atlantic salmon of Baltic sea stock acclimated to 11–14°C selected about 16°C. It is necessary to point out, however, that in both of the foregoing cases, the fish were very young; two months in the case of Mantleman and not quite out of the yolk sac stage in the case of Fisher and Elson. While the question seems not to have been investigated seriously, there is some evidence to suggest that other things being equal, the younger fish of species select a higher temperature than do older ones (Fry, 1937; Ferguson, 1958).

Another, and, in our opinion, more likely explanation for the above-mentioned discrepancy stems from some of the physical properties of our apparatus. In order to establish a suitable thermal gradient in the water, it was necessary to maintain the metal bottom of the trough at a higher temperature than that of the water flowing immediately above it. This seems not to have been a feature of the apparatus used by Mantleman (1958) and was definitely not a problem for Fisher and Elson (1950) since they used a still-water gradient. In our experiments, therefore, it is highly possible that the fish were, with respect to temperature, orienting to the substratum as well as to the surrounding water. If such was the case, the selected temperature, as measured by ambient temperature, would always tend to underestimate the true value.[5]

The physiological basis for the action of DDT is as yet obscure. There is, however, considerably less uncertainty as to its site of action. Although DDT has ready access to all the organs of the body immediately following exposure (Premdas and Anderson, 1963), there is considerable evidence which points to the nervous system as being the target organ system (O'Brien and Matsumura, 1964). Since the nervous system is also the chief mediator of the temperature selection response (Fisher, 1958), our results which show a relationship between DDT action and a behavioural response to temperature are not unexpected.

The special significance of our results relates to the fact that, as far as we are aware, this is the first time it has been reported that a chemical treatment can induce a shift in the selected temperature. The apparent dependence of the sign of the response upon the concentration of DDT is puzzling, and is likely to remain so until such time as more is known about its biochemical action. Perhaps of some significance is recent work which shows that DDT can alter the level of NAD-kinase in *Triatoma infestans*, low and high doses of DDT resulting in a decrease and increase, respectively, of this enzyme (Ilevicky *et al.*, 1964).

The violent muscular reflex response characteristic of the cold response is interesting because it seems to be similar to the kind of response described

[5]Recent evidence in the laboratory of one of us (J. M. A.) supports this hypothesis. In a new apparatus, specifically designed to increase the efficiency of the heat exchange between the bottom of the trough and the overhead moving water, salmon acclimated to 10°C selected 11–13°C. The DDT effect was still very much evident, e.g. 24-hr exposure to 10 ppb and 100 ppb DDT resulted in selected temperatures of 5–7°C and 21–23°C, respectively.

by Roots and Prosser (1962) at the temperature which brings about a cold-blocking of a simple reflex in goldfish. They concluded that the site of the cold-block was in the central nervous system. Our results, therefore, suggest that the DDT in these experiments is acting upon central, rather than peripheral, nervous structures.

While the problem was not specifically investigated in this work, it seems highly likely from the results dealing with the DDT-induced cold response, that pretreatment with DDT raises the lower lethal temperature under certain conditions. These conditions, it will be recalled, involve a relatively warm acclimation (which would tend to increase the sensitivity to cold and thus allow a DDT-effect to be more easily noted) and relatively high DDT concentrations (which raise the selected temperature). Under natural conditions an increase in both the lower lethal temperature and the selected temperature are brought about by an increase in acclimation temperature. In our work no such change in acclimation temperature occurred. It suggests DDT somehow interfered with the normal thermal acclimation process. If such were indeed the case, it seems clear that further work in the field may do much to elucidate the nature of thermal acclimation mechanisms.

ACKNOWLEDGMENTS

We are grateful to the Fisheries Research Board of Canada which supported this work through a Research Contract with the University of New Brunswick, and to the Fish Culture Branch, Department of Fisheries of Canada for supplying Atlantic salmon from the hatchery at East Florenceville, N. B. One of us (D. M. O.) wishes to express his appreciation to the National Research Council of Canada for financial support in the form of an NRC Studentship.

REFERENCES

BRETT, J. R. 1952. Temperature tolerance in young Pacific salmon. *J. Fish. Res. Bd. Canada*, **9**(6): 265–323.

FERGUSON, R. G. 1958. The preferred temperature of fish in their midsummer distribution in temperate lakes and streams. *J. Fish. Res. Bd. Canada*, **15**(4): 607–624.

FISHER, K. C. 1958. An approach to the organ and cellular physiology of adaptation to temperature in fish and small mammals, pp. 3–49. *In* C. Ladd Prosser [ed.] Physiological adaptation. American Physiological Society, Washington, D.C.

FISHER, K. C., AND P. F. ELSON. 1950. The selected temperature of Atlantic salmon and speckled trout and the effect of temperature on the response to an electrical stimulus. *Physiol. Zool.*, **23**(1): 27–34.

FRB. 1961. *Annual Report of the Fisheries Research Board of Canada* for 1960–61, 192 pp., Ottawa.

FRY, F. E. J. 1937. The summer migration of the cisco, *Leucichthys artedi* (LeSueur), in Lake Nipissing, Ontario. *Univ. Toronto Stud., Biol. Ser.*, No. 44 (*Pub. Ontario Fish. Res. Lab.*, No. 55), 91 pp.

1947. Effects of the environment on animal activity. *Ibid.*, No. 55 (*Ibid.*, No. 68), 62 pp.

HOLDEN, A. V. 1962. A study of the absorption of C^{14}-labelled DDT from water by fish. *Ann. Appl. Biol.*, **50**: 467–477.

ILEVICKY, J., M. L. DINAMARCA, AND M. AGOSIN. 1964. Activity of NAD-kinase of nymph *Triatoma infestans* upon treatment with DDT and other compounds. *Comp. Biochem. Physiol.*, **11**(3): 291–301.

MANTLEMAN, I. I. 1958. O respredelenii molodi nekotorykh vidov ryb v termogradientnykh usloviiakh. [Distribution of the young of certain species of fish in temperature gradients.] *Izvestiia Vsesoiuznogo Nauchno-Issledovatelskogo Instituta Ozernogo i Rechnogo Rybnogo Khoziaistva*, **47**(1): 1–63. [Fish. Res. Bd. Canada, Translation Series, No. 257, 1960.]

O'BRIEN, R. D., AND F. MATSUMURA. 1964. DDT: a new hypothesis of its mode of action. *Science*, **146**(3644): 657–658.

PITT, T. K., E. T. GARSIDE, AND R. L. HEPBURN. 1956. Temperature selection of the carp (*Cyprinus carpio* Linn.). *Canadian J. Zool.*, **34**(6): 555–557.

PREMDAS, F. H., AND J. M. ANDERSON. 1963. The uptake and detoxification of C^{14}-labelled DDT in Atlantic salmon, *Salmo salar*. *J. Fish. Res. Bd. Canada*, **20**(3): 827–837.

ROOTS, B. I., AND C. L. PROSSER. 1962. Temperature acclimation and the nervous system in fish. *J. Exp. Biol.*, **39**(4): 617–629.

ROZIN, P. N., AND J. MAYER. 1961. Thermal reinforcement and thermoregulatory behaviour in the goldfish, *Carassius auratus*. *Science*, **134**(3483): 942–943.

SULLIVAN, C. M., AND K. C. FISHER. 1953. Seasonal fluctuations in the selected temperature of speckled trout, *Salvelinus fontinalis* (Mitchill). *J. Fish. Res. Bd. Canada*, **10**(4): 187–195. 1954. The effects of light on temperature selection in speckled trout, *Salvelinus fontinalis* (Mitchill). *Biol. Bull.*, **107**(2): 278–288.

Retinomotor Changes in Flatfishes[1,2]

By J. A. C. Nicol

The Marine Biological Laboratory, Plymouth, England

ABSTRACT

This histological study is concerned with demonstrating the existence of retinomotor changes in flatfishes. In three species, selected as representatives (sole, *Solea solea*; plaice, *Pleuronectes platessa*; and merry sole, *Microstomus kitt*), it is shown that normal radial displacements of rods, cones, and retinal pigment take place in expected directions in light and darkness, with exceptions which may be important but whose implications have still to be revealed. In the plaice the cones of the dorsal retina are permanently retracted against the basement membrane, and mobile elsewhere. The eyes of flatfishes, therefore, conform to those of other teleosts in photomechanical responses to illumination.

INTRODUCTION

In the retina of many teleost fishes the cells of the pigment epithelium contain a dark retinal pigment and bear processes which extend inwards between the receptor elements, *viz.* the rods and cones (Fig. 1). The pigment and the receptors execute movements, collectively termed retinomotor, under the influence of light and other factors. In darkness the retinal pigment moves outwards, towards the base of the pigment cell (withdrawal); in light the pigment moves inwards, towards the external limiting membrane (extension). When movements of rods and cones occur, the myoids of the rods contract and those of the cones elongate in dim light or darkness; in light the myoids of the rods lengthen and those of the cones contract. These several movements bring about radial displacement of the outer segments of the rods and cones.

Retinomotor movements occur in freshwater and neritic marine teleosts; they are slight or absent in deep-water species (Walls, 1942; Ali and Hanyu; 1963; O'Connell, 1963). In the eel the rods alter whereas the cones are static (Garten, 1907). In flatfishes (Heterosomata) it was believed that only the retinal pigment moved (Bayliss *et al.*, 1936; *cf.* Walls, 1942), but it has since been shown that the cones of the sole (*Solea solea*) shorten and lengthen in light and darkness, respectively (Nicol, 1961).

In the present investigation a study was made of the receptor elements and the pigment epithelium of three selected species of flatfishes in order to determine to what extent retinomotor changes take place in this group of fishes.

The types of cones and their arrangements in the retinae of some flatfishes have been described by Engström and Ahlbert (1963) and by Engström (1963).

[1]Received for publication September 21, 1964.
[2]This is paper II in a series: Photomechanical changes in the eyes of fishes.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

They found single cones and double cones with approximately equal components in *Pleuronectes platessa*, *Platichthys flesus*, *Microstomus kitt*, and *Limanda limanda* (all placed in the genus *Pleuronectes* by these authors), and in *Solea solea* and *Hippoglossoides platessoides*. Triple cones occur in the dorsal region of all these species except *P. flesus*; in *S. solea*, triple cones are distributed over the whole retina. The density of double cones in *P. platessa* is greatest in a region slightly dorsal and posterior to the optic nerve. In vertical section through the centre of the eye of the plaice, cone densities are least in the ventral region, below the optic nerve, increasing to a maximum in a region

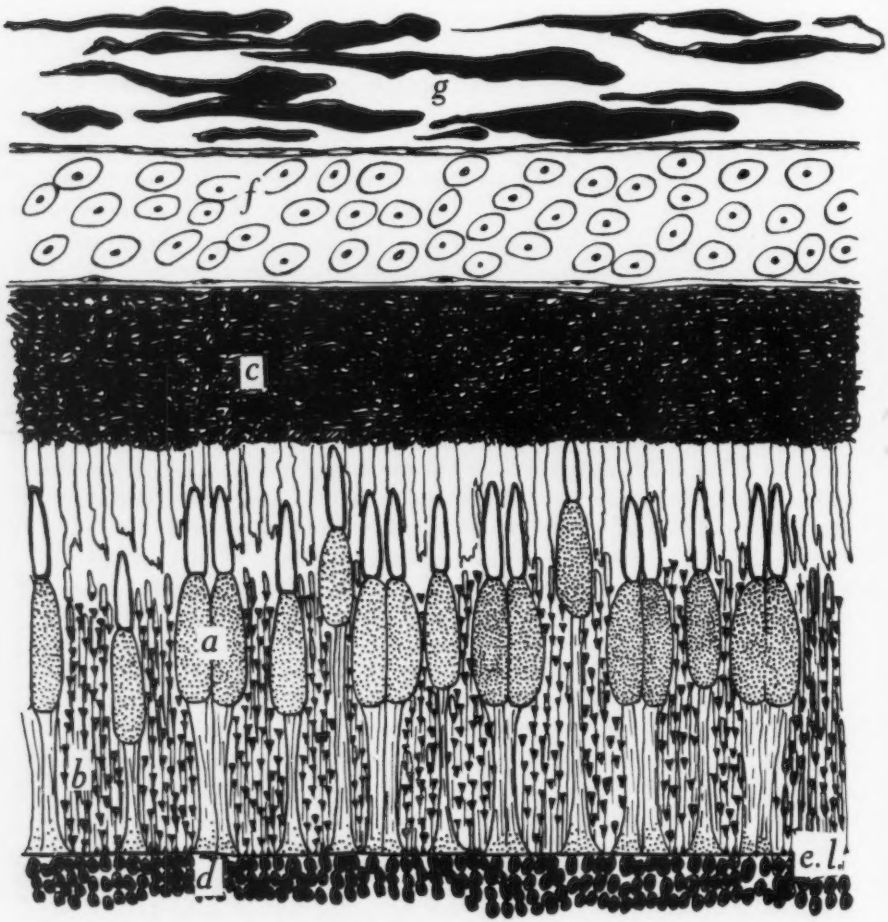


FIG. 1. Section through the central fundus of a plaice eye. Dark-adapted condition. *Legend*: a, cones; b, rods; c, pigment epithelium; d, nuclear layer; e.l., external limiting membrane; f, choriocapillaris; g, chorioid. × 965.

above the optic nerve (about one-third of the distance between the optic nerve and the ora), and lower again in the dorsal retina. Engström and Ahlbert have presented extensive data concerning cone densities and fig. 6 of their paper of 1963 is relevant. Ellipsoids of the double cones of *Pleuronectes* are thinner in regions of high density (Engström, 1963, fig. 32).

MATERIALS AND METHODS

Flatfishes whose eyes were examined in the present study were plaice (*Pleuronectes platessa*), lemon or merry sole (*Microstomus kitt*), and sole or common sole (*Solea solea*) (Marine Biological Association, 1957). This research was started in 1959, and over 90 flatfishes have been examined during the past 5 years.

The fish were kept in tanks standing in a light-tight room and containing running sea water. Fish were subjected to various periods of light and darkness, the durations of which corresponded to those employed in a previous investigation (Nicol, 1961).

Dark-adaptation: ½ hr, 1430–1500 hr; 1 hr, 1430–1530 hr;
2 hr, 1430–1630 hr in darkness.
17 hr, 1630–0930 hr; 19 hr, 1700–1200 hr; 31 hr, 1700 (first day)–2400 hr (second day) in darkness.

Light-adaptation: ½ hr; 0930–1000 hr; 1 hr, 0930–1030 hr;
2 hr, 0930–1130 hr in the light.

Illumination was provided by 100-w photoflood or 150-w shop-illumination lamps, one over each tank, at distances of 0.7–1.5 m. The sides and bottom of the tanks were dark in hue. Fish were placed in the tanks in the evening and lights were turned on next day, if desired. At least three flatfishes were used for each experiment. The temperature of the aquarium tanks was held at 15°C. All experiments were carried out during autumn, winter, and spring, and none during summer time, because of the difficulty of cooling water when ambient temperatures rose above 15°C.

Eyes were examined histologically, fixed in Bouin's or Helly's fluids, and sectioned in celloidin and wax. Sections were cut transversely and dorsoventrally through the centre of the eye. Bleaching of retinal pigment, when necessary, was carried out with potassium permanganate followed by oxalic acid. Stains used were Ehrlich's haematoxylin and eosin plus Biebrich scarlet, lissamine violet AVS (British Drug Houses), Masson's trichrome, and Heidenhain-azan.

Conventional terminology for referring to the orientation of parts of the eye has been adopted. Inwards, inner, and internally mean towards the centre of the eye; outwards, outer, and externally mean away from the centre of the eyeball. Movement of pigment distally, pigment extension or expansion refer to migration of retinal pigment from the cell body or base of the pigment cell towards the centre of the eye (i.e. centripetally or inwards). Movement

of pigment proximally, retraction or retreat, refer to migration of retinal pigment towards the base of the cell (i.e. outwards). It is generally held that the pigment granules of the pigment cells move to and fro in fixed or permanently extended processes (Parker, 1932). Myoids or rods and cones contract and extend, thereby causing the rods and cones to shorten or elongate (lengthen), while their outer segments are moved inwards or outwards, respectively.

When a pigment index is used, it has the following significance: 1, pigment basal, fully retracted; 2, $\frac{1}{4}$ expanded; 3, $\frac{1}{2}$ expanded; 4, $\frac{3}{4}$ expanded; 5, fully expanded (or extended).

OBSERVATIONS

PLAICE, *Pleuronectes platessa*

The outer layer of the retina (the receptor layer plus the pigment layer) is thin near the ora (about 20 μ across) and increases to maximal thickness (about 110 μ) in a region slightly above the centre of the fundus (measurements made in an eye having a vertical diameter of 11 mm). The thickness of the receptor layer alone changes from 15 μ to 90 μ from the periphery towards the central fundus, somewhat above the optic nerve (Fig. 2 and 3). In the dorsal fundus the cones are more closely packed and possess thinner and more elongate ellipsoids than in the central fundus (Fig. 4 and 5). Single and double cones occur; the rods are very thin (Fig. 3). The retinal pigment, when expanded, extends to the ellipsoids of the cones, and in the ventral and central region it often extends further, between the cone myoids and up to the external limitans (Fig. 4 and 5). When fully expanded the pigment granules are most dense between the outer segments of the cones.

PIGMENT. In darkness the retinal pigment retreats into the basal regions of the pigment cells (Fig. 2 and 3). Most of the retinal pigment is withdrawn in $\frac{1}{2}$ hr (pigment index 1–2), and retraction is complete in 1 hr. In the light it extends inwards to the myoids of the cones, or further; the rods are covered by this migration (Fig. 4 and 5). Extension of the retinal pigment is largely or fully completed in $\frac{1}{2}$ hr (pigment index 4–5), and fully completed in 1 hr (index 5).

CONES. The cones in the dorsal retinae of dark-adapted fish invariably remain shortened against the external limiting membrane (Fig. 2). Elsewhere they become extended when the eye is dark-adapted (Fig. 3). Both single and double cones suffer displacement, and single cones often shift further outwards than double cones (Fig. 3). Extension is partial in the central and ventral retina after $\frac{1}{2}$ hr, and completed in 1 hr. The cones shorten in the eyes of illuminated fish. They are retracted or slightly extended after $\frac{1}{2}$ hr, and fully shortened after 1 hr (Fig. 5).

RODS. In darkness rods become retracted, some of them close to the external limiting membrane; this shortening occurs in $\frac{1}{2}$ hr (Fig. 3). In the light the rods become extended in all regions of the retina by 1 hr (Fig. 6). This movement displaces the outer segments of the rods beyond the ellipsoids of the cones and within the fringes of the advancing pigment.

MERRY SOLE, *Microstomus kitt*

Retinal pigment, cones, and rods are mobile in the merry sole. Cones are more numerous in the central than in the dorsal and ventral retina. Also, the outer region of the retina, comprising receptor layer plus pigment epithelium, is thicker in the central fundus: in an eye 9 mm high it is 90 μ thick in the central fundus and 25 μ in the dorsal and ventral retina. The receptor layer alone is 18 μ in thickness dorsally and ventrally, and 70 μ in the central fundus. The outer segments of the twin cones move together during photomechanical changes. In the dorsal retina, towards the ora, the large cones extend across the outer retinal layer to the base of the pigment epithelium; the cones here are about 18 μ long, and inner and outer segments are 10 μ and 8 μ, respectively. When fully extended the retinal pigment reaches the myoids of the cones, screening the rods and separating the outer segments of the cones from each other. After prolonged exposure to light the retinal pigment becomes concentrated in the distal regions of the cell processes.

RETINAL PIGMENT. The pigment usually becomes retracted in darkness and extended in light. In retinae of dark-adapted fish, retraction was still incomplete after ½ hr in darkness (indices, central 2–3, ventral 4–5) and fully complete after 1 hr (Fig. 7). The retinal pigment was fully retracted after prolonged periods in darkness (17–31 hr) (Fig. 8). Following ½ hr of illumination the pigment was partially extended (indices 2–4); it was fully extended after 1–2 hr in the light (Fig. 9 and 10).

CONES. Cones in the extreme dorsal retina within 15 μ of the ora remain contracted against the external limitans in darkness. Since the cones in this region extend right across the receptor layer of the retina, they appear to have little or no room for movement. Elsewhere they lengthen in darkness and shorten in light, with exceptions to be noted.

After ½ hr in darkness cones were still retracted. Following longer periods in darkness cones were extended in half the fish examined and partially extended or retracted in the remainder (Fig. 7 and 8). These were fish held in darkness for 1 or 2 hr or overnight. In two fish held in darkness for 31 hr (to 2400 hr), cones were extended. Single cones were often extended further than double cones. After ½ hr in the light, cones were partially extended in one fish, and retracted in two fish. Cones were fully retracted after 1–2 hr in the light (Fig. 9–11).

There is no doubt that the cones are motile in the central and ventral retina and that they do shorten against the external limitans when the fish is illuminated during daylight hours; they are also capable of elongating (except in the extreme dorsal retina) when the fish is kept in darkness. Nevertheless, the behaviour of the cones when subjected to darkness during normal daylight hours is somewhat irregular. It is interesting that in some of these fish the several motile elements of the retina obviously behaved independently of each other: both rods and cones were shortened and pigment was retracted.

RODS. Rods shorten in darkness, some of them coming to the external limitans, and they elongate in the light, becoming displaced beyond the cone ellipsoids (Fig. 7 and 11).

COMMON SOLE, *Solea solea*

In a previous paper (Nicol, 1961) it was reported that retinomotor changes take place in the sole: pigment expands in the light and retracts in darkness, and cones shorten in the light and lengthen in darkness.

As in the merry sole there were many exceptions for, whereas the cones consistently shortened when illuminated, they often failed to elongate in darkness. Cones were elongated, pigment retracted, and rods shortened in fish killed at midnight, after 31 hr in darkness.

More material now being available, it is possible to amplify this account. Single and double cones can be distinguished in transverse sections of the retina (Fig. 13). Both components of the double cones move together, and single as well as double cones elongate in darkness (Nicol, 1961, plate I, fig. 1).

It was possible to distinguish rods and to follow their movements in bleached sections. In darkness rods were shortened and withdrawn to the external limiting membrane (Fig. 12). After illuminating eyes ½ hr, rods were extended in two fish and retracted in one. Longer periods of illumination usually caused the mass of rods to become displaced towards the ends of the cone myoids or the cone ellipsoids (Fig. 13).

DISCUSSION

This research originated with an intention of investigating the factors controlling photomechanical changes in the eyes of fishes, namely occlusion of the selachian tapetum and retinomotor changes in teleosts, and investigations of this nature are still being actively pursued. For several reasons — availability, hardiness, *inter alia* — flatfishes were chosen for the teleost experiments, and a search of the literature indicated that only the retinal pigment shifted in the eyes of these animals, the rods and cones being static. There has also been some implication that the limited retinomotor activity may be correlated with pupillary mobility (Walls, 1942). Pupillary closure is not general among flatfishes, however, and among local species (i.e. in the English Channel) it occurs in the brill and the turbot, and not in the plaice, sole, and merry sole (Bateson, 1890). Since it was necessary to establish the degree and course of retinomotor changes in normal animals, flatfishes were illuminated or kept in darkness. In the three species selected for study — plaice, sole, and merry sole — it became apparent that not only does the retinal pigment perform radial excursions, expanding in light and retreating in darkness, but that the rods and cones move as well. The cone myoids shorten and their ellipsoids are pulled close to the external limiting membrane in the light, and the ellipsoids with their outer segments are pushed outwards in darkness.

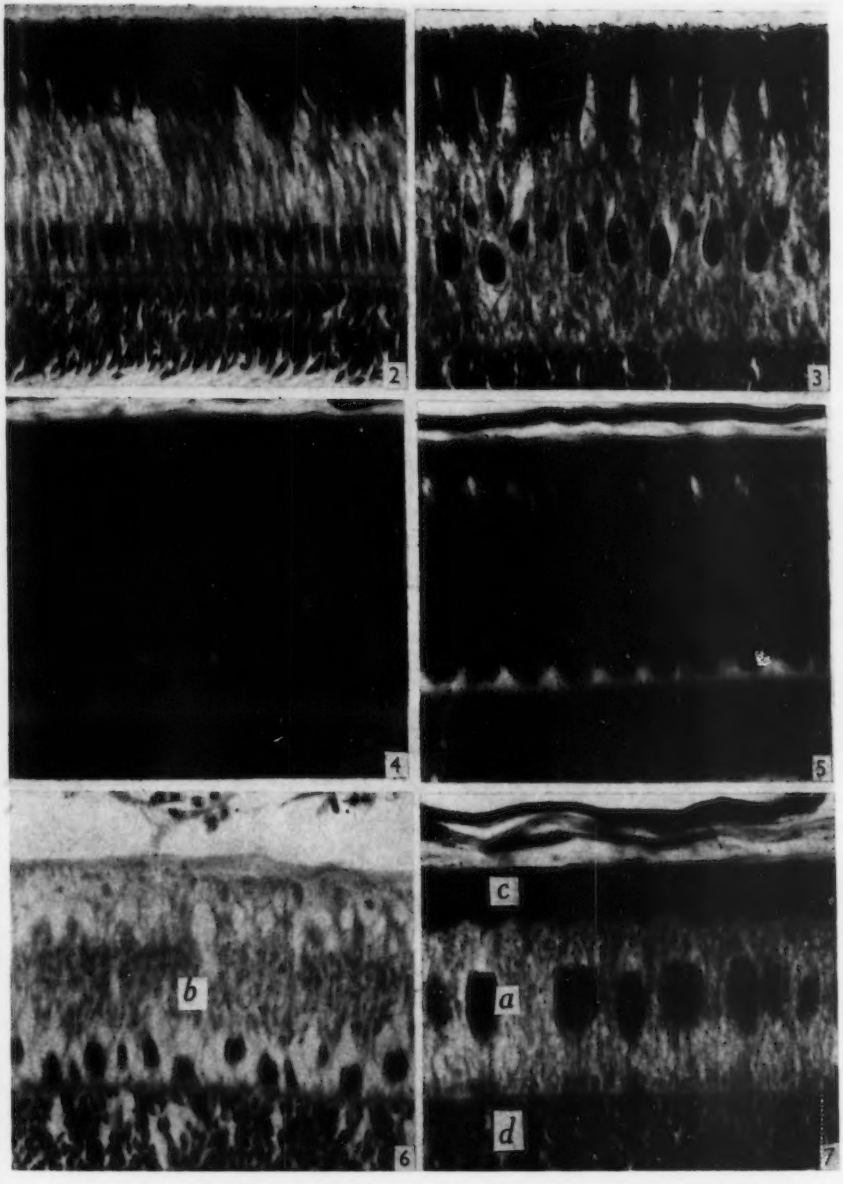


FIG. 2–7. Photographs of sections through the eyes of flatfishes (Fig. 2–6: eyes of plaice, *Pleuronectes platessa*). Fig. 2: Darkness 2 hr. Dorsal retina. Cones static; rods retracted; pigment withdrawn. Fig. 3: Same eye, centre of retina. Double and single cones extended; rods retracted; pigment withdrawn. Fig. 4 and 5: ½ hr in the light; dorsal and central retina, respectively. Fig. 6: Light 6 hr. Bleached section. Cones shortened; rods extended. Fig. 7: Merry sole, *Microstomus kitt*. Darkness 2 hr. Centre of retina. Cones extended; rods shortened; pigment withdrawn. Fig. 2, 3, 6, 7, × 440; Fig. 4 and 5, × 378. *Legend*: a, cones; b, rods; c, pigment epithelium; d, nuclear layer.

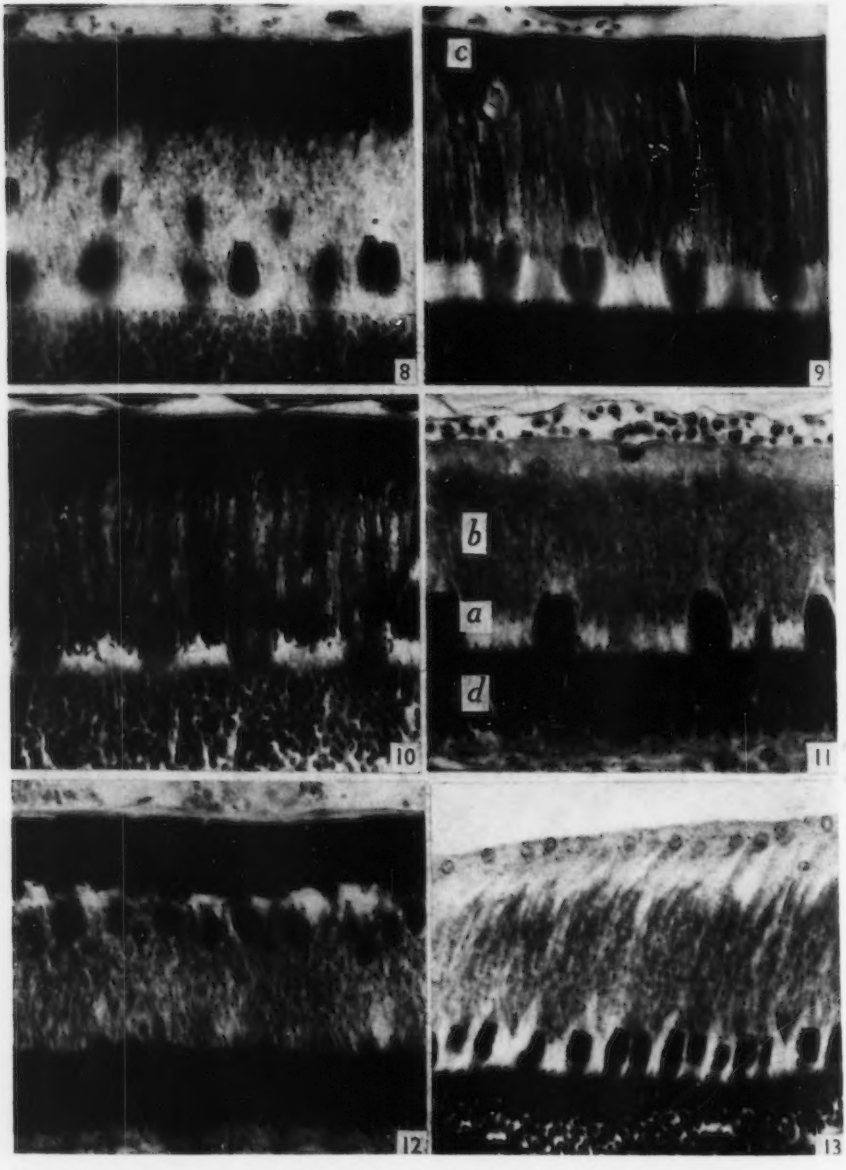


FIG. 8–11. Eyes of merry sole, *Microstomus kitt*. Fig. 12 and 13. Eyes of sole, *Solea solea*. Fig. 8: Darkness overnight, 1700 hr to 1200 hr. Rods retracted; single cones in part extended; double cones largely shortened. Fig. 9: Light ½ hr. Cones shortened; pigment partially extended. Fig. 10: Light 2 hr. Cones retracted; rods extended; pigment fully expanded. Fig. 11: Light 2 hr. Bleached section. Rods extended. Fig. 12: Dark 1 hr. Rods retracted; double and single cones fully extended. Fig. 13: Light 2 hr. Bleached section. Rods extended. All photographs of the centre of the retina. × 440.

In flatfishes which have been illuminated for ½ hr, pigment movement is still incomplete and, although the pigment may extend through the entire length of the cell processes, it may still be sparse. After 1 hr, pigment extends to its maximal extent and density, sometimes accumulating in the distal regions of the cell processes, between the outer segments of the cones and the ellipsoids. Maximal shortening of the cones occurs between ½ to 1 hr.

Movements of the rods take place concomitantly with those of the cones. Now, the outer segments of the rods are quite short, about 10 μ, and they are staggered in considerable depth, across 40 μ or so of the outer receptor layer. In darkness the innermost rods are pulled down to the external limiting membrane; in light these same rods are pushed outwards beyond the ellipsoids of the cones. In darkness all the rods, from the external limitans to the bases of the pigment epithelial cells, are cleared of obscuring retinal pigment; and in light all the rods are buried in pigment.

There is much irregularity in the extent to which cones move during darkness in the eyes of sole and merry sole, elongation being often partial or incomplete. It is possible that these divergencies from the expected pattern are indicative of persistent diurnal rhythmicity operating independently of direct or immediate stimulatory factors, but no controlled experiments were made to investigate this contingency.

The functional significance of these observations should now be considered. It seems very probable that the expansion of pigment inwards when the eye is illuminated, by shielding the rods, precludes bleaching of the visual pigment or, putting the matter less committedly, holds the rods in a dark-adapted condition. Nevertheless, critical experiments to test this hypothesis by measuring pigment densities have still to be carried out. Furthermore, the outward displacement of the innermost rods means that they are pushed well into the advancing pigment. The outward movement of cones in eyes experiencing darkness clears the light path to many or all the rods, and may be an important factor at very low light intensities.

ACKNOWLEDGMENTS

Grateful acknowledgment is made to Mr A.C.G. Best for making the histological preparations and for the photomicrography of what often proved to be difficult or intractable material. Mr R. G. Maddock helped with many of the experiments.

REFERENCES

Ali, M. A., and I. Hanyu. 1963. A comparative study of retinal structure in some fishes from moderately deep waters of the Western North Atlantic. *Canadian J. Zool.*, **41**: 225–241.

Bateson, W. 1890. The sense-organs and perceptions of fishes; with remarks on the supply of bait. *J. Marine Biol. Assoc. U.K.*, **1**: 225–256.

Bayliss, L. E., R. J. Lythgoe, and K. Tansley. 1936. Some new forms of visual purple found in sea fishes with a note on the visual cells of origin. *Proc. Roy. Soc. London*, B, **120**: 95–113.

ENGSTRÖM, K. 1963. Cone types and cone arrangements in teleost retinae. *Acta Zoologica*, **44**: 179–243.

ENGSTRÖM, K., AND I.-B. AHLBERT. 1963. Cone types and cone arrangement in the retina of some flatfishes. *Acta Zoologica*, **44**: 119–129.

GARTEN, S. 1907. Die Veränderungen der Netzhaut durch Licht. Handbuch der gesamten Augenheilkunde (Graefe, Saemisch). 2 Aufl. (1925), Bd. 3, 250 pp. Springer, Berlin.

MARINE BIOLOGICAL ASSOCIATION. 1957. Plymouth Marine Fauna. Marine Biological Association of the United Kingdom, Plymouth, England.

NICOL, J. A. C. 1961. Photomechanical changes in the eyes of fishes. I. Retinomotor changes in *Solea solea*. *J. Marine Biol. Assoc. U.K.*, **41**: 695–698.

O'CONNELL, C. P. 1963. The structure of the eye of *Sardinops caerulea*, *Engraulis mordax*, and four other pelagic marine teleosts. *J. Morph.*, **113**: 287–329.

PARKER, G. H. 1932. The movements of the retinal pigment. *Ergebnisse der Biologie*, **9**: 239–291.

WALLS, G. L. 1942. The vertebrate eye and its adaptive radiation. *Bull. Cranbrook Inst. Sci.*, No. 19. Bloomfield Hills, Michigan.

Food and Growth of Fishes. I. A Growth Curve Derived from Experimental Data[1]

By J. E. Paloheimo and L. M. Dickie

Fisheries Research Board of Canada
Biological Station, St. Andrews, N. B.

ABSTRACT

A general equation for growth of fishes is obtained through use of the relations among body weight, metabolic rate, and growth efficiency that have been found in laboratory experiments. The curves show an early inflection point and gradually decreasing growth rate thereafter, without a theoretical asymptote. When growth efficiency is constant this equation indicates that growth becomes nearly exponential and is fitted exactly by the Parker and Larkin (1959) equation. When growth efficiency decreases with increasing rations the curves become more complex, as described here.

Growth curves having an asymptote, such as the von Bertalanffy curve, have often been fitted to growth data. When the estimated asymptote can be related to the inflection point of the early part of a growth phase, it is proportional to a physiological time scale suggested by the food–growth relations. Truly asymptotic growth would appear to result only from complex changes in metabolism, growth efficiency, or interactions with mortality of the sort suggested by Lee's phenomenon.

Some consequences of these results of food–growth experiments are discussed in relation to studies of biological productivity, especially their bearing on objectives of fisheries management. They suggest that, in general, highest sustained yield from a particular growth phase or stanza is obtained from a type of cropping which results in a population of fish having an average size near that of the smallest fish in the stanza.

Any dynamic growth process, such as the growth of fishes, is a result of those processes tending to increase and decrease the body mass. This truism is the logical basis for all attempts to understand the mechanisms underlying growth, or indeed all general biological production systems. The specific investigations take several forms. Weiss and Kavanau (1957), with particular interest in growth and differentiation of body tissues, have outlined a concept of the basic mechanism in terms of elementary reacting biochemical particles and inhibiters within the developing and growing system. From the properties of the resulting model in some five parameters and initial conditions they deduce consequences of compensatory growth and differentiation in accord with experimental observations. In a different approach, von Bertalanffy (1938, 1957), with an interest in metabolism and growth of whole animals, identifies the processes of increase and decrease as anabolism and catabolism. That is

$$\frac{dW}{dt} = HW^m - DW^n \qquad (1)$$

[1]Received for publication October 28, 1964.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

where H and D are coefficients of the rates of anabolism and catabolism and W is body weight. Following Rubner, he postulated that the rates in fishes must be related to the surface area and body mass, hence put $m = 2/3$ and $n = 1$. The task of data fitting, given the resulting growth equation in only two parameters and one initial condition, is a relatively simple matter. Since the time that its application to fish growth data was illustrated by Beverton and Holt (1957), there have been many publications purporting to show that it provides adequate expression of growth of particular species of fish at least during the exploited phases of their life history.

There is no doubt of the value of general growth curves for the description and comparison of growth observations of different organs or species at different times or places. It is the biological interpretation of the parameters describing the statistical fittings that is problematical. The Weiss-Kavanau model is developed independent of explicit consideration of the organism's interaction with the external environment and is thus of limited heuristic value in physiological ecology. In the case of the von Bertalanffy curve, Richards (1959) rejected the validity of simple physiological interpretation. Parker and Larkin (1959) used an exponential-type expression as an empirical description of growth within life-history "stanzas" and found it to fit back-calculated growth data for several species of salmonids. The von Bertalanffy curve appeared applicable to parts of the same data, but only under the frequently used sampling restriction that size at age be determined from the present (i.e. observed) average length of the age-groups in the population sample; it did not describe the growth derived from back-calculations of scale markings. But where the two methods give different results, technically satisfactory back-calculations are more likely to represent population growth rates, free from natural selectivity or sampling bias with respect to size. It is evident from such contradictions that biological interpretation of fitted mathematical growth parameters requires reference to experimental as well as field study — to the extent that any postulated mechanisms can be identified and measured experimentally.

An alternative, more direct approach than that of Weiss and Kavanau or von Bertalanffy seems to us to have been insufficiently explored. That is, as pointed out by Winberg (1956) among others, the basic energy equation may be written as

$$\frac{\Delta W}{\Delta t} = R - T \qquad (2)$$

where the energy equivalent of growth, ΔW, during any period of time, Δt, is simply the difference between the energy acquired in the rations, R, and the total metabolic energy expenditure, T, measured over the unit of time. In place of the abstract concepts of anabolism and catabolism, which necessitate a somewhat arbitrary specification of their relation to body weight, we thus have three quantities which are clearly open to experimental study:

growth, food intake, and total metabolism. If measurements of these variables in common energy units are valid, they must balance as in equation (2).

Given variables which can be experimentally determined, the problem of constructing growth curves is then to define their relation to body weight from experiments and to express this in appropriate terms in the energy equation. In this paper we use relations derived from metabolism, growth, and feeding experiments in this way. We discuss some of the implications of the resulting growth curves for studies of biological production, especially their relation to the yield from exploited fish populations.

GROWTH AND METABOLISM

The metabolism of fishes as reflected in the rate of oxygen consumption has been extensively studied and found to be well described by a relation of the form

$$\begin{gathered} T = \alpha W^{\gamma} \\ \text{whence } \log T = \log \alpha + \gamma \log W \end{gathered} \tag{3}$$

where W is body weight, α is a constant defining the level of metabolic expenditure per unit time (i.e. the antilog of the linear logarithmic relationship when $W = 1$), and γ defines the rate of change of metabolism with body weight (i.e. the slope of the log line). The logarithmic relationship $\log T = \log \alpha + \gamma \log W$ will, in later discussion, be referred to as the T-line. Winberg found that this relation was equally well fitted by conversion of the difference between rations and weight gains into O_2 equivalents or calories. Using similar calculations in a review of the data of a number of feeding experiments (Paloheimo and Dickie, 1965a, in preparation), we have found that on a maintenance diet the value of α, specifying the level of total metabolism of fishes, is close to standard metabolism as measured from the oxygen consumption. At maximum or *ad libitum* feeding rates the measured total metabolism approaches the active level as defined by Job (1955) and Fry (1957). Furthermore, feeding at intermediate levels appears to result in intermediate metabolic levels. That is, at a particular level of food abundance and availability at a particular temperature, fish of different sizes appear to adjust their various components of metabolism and feeding to more or less stable levels, resulting in a particular value of α. A different value of α results from a different food or temperature level but the value of γ is unaffected. For a given type and rate of food supply we may therefore write

$$T = \alpha W^{\gamma} Q^{t^{\circ} - t_0}$$

where t° is the temperature measured about a constant value t_0 which thus permits its expression as a log-linear effect over the observed temperature range, and Q is a constant having a value close to the Krogh correction value for a particular temperature range. In this paper we consider that we are deal-

ing with constant temperatures, hence write this relationship in the form of equation (3). From numerous experiments it appears that an adequate working value for $\gamma = 0.8$ and the level of metabolism α may take values between those for standard and active metabolism, depending on the level of the food supply.

We have thus, on the basis of direct experimental evidence, a relationship between the metabolic component of equation (2) and the body size of fish. Rewriting the equation in the form

$$\frac{\Delta W}{\Delta t} = R - \alpha W^{\gamma} \tag{4}$$

we have a possible starting point for deriving a growth equation if we have similar information on the changes in R.

In considering this problem, Ivlev (1944) found that at given body size the rate of travel during grazing was generally unaffected by food concentration. But as food concentration increased, the ration obtained increased at a decreasing rate, suggesting (Ivlev, 1961) a progressive drop in grazing efficiency. These relationships were expressed in the form

$$\frac{dR}{dp} = \xi (R_m - R)$$

$$\text{whence } R = R_m (1 - e^{-\xi p})$$

where R is the ration, p is the food concentration, R_m the maximum ration which the fish can obtain at very high food concentrations, and ξ a coefficient of proportionality. The adequacy of this expression was checked experimentally on several species of fishes although with a limited size range (Ivlev, 1955). If it holds over a wide size range, then, in considering growth, we have the problem of determining the relationship between body size and the maximum ration R_m. It is not at all clear how the interaction of physiological and behavioural characteristics of different sizes of fish with their ecological opportunities for food-getting would determine this relationship, either in terms of their grazing efficiency, the distance travelled, or the rate of travel. The problem is further complicated by Ivlev's (1955) finding that the ration obtained varied with the degree of dispersion of the food particles within the searched area.

Equation (4) implies, however, that for any growth to take place $R > \alpha W^{\gamma}$. If initially we put $R = \beta W^{\gamma}$, then from equation (4) we arrive at the growth equation discussed by Parker and Larkin. In a later section we conclude that under special circumstances this curve does in fact provide an apt description of fish growth. However, there is no *a priori* reason for assuming that ration intake will follow such a simple relationship. For illustration we consider the increase in workload necessary to obtain food with increasing size in three

logically possible cases: (1) fish meet their food requirements without increasing either swimming speed or distance travelled; (2) by increasing only the distance, hence the total time, travelled; or (3) by increasing only the swimming speed (i.e. keeping the total time constant). In actual fact, of course, fish are most likely to obtain food by combinations of these methods, resulting in feeding by a series of sudden darts and stops. Lacking specific experimental observations we will not attempt detailed discussion of this logically complex situation with its implied components of acceleration.

Bainbridge (1961) gives the drag on a fish-shaped object moved through water as

$$\sim AV^2C_f$$

where A is the cross-sectional area of the fish, which is proportional to L^2 where L is the length; V is the velocity or speed of swimming; and C_f is the coefficient of drag. For the more efficient laminar (as opposed to turbulent) flow of water over the surface of the fish

$$C_f \sim \frac{1}{L^{1/2}V^{1/2}} \sim \frac{1}{W^{1/6}V^{1/2}}.$$

Since case (1) assumes constant swimming speed and distance travelled, the work is proportional to the drag

$$\sim L^2/L^{1/2} = L^{3/2} \sim W^{1/2}.$$

In case (2)

work $\sim$ drag $\times$ distance travelled $\sim W^{1/2} \times W^{\gamma} = W^{1/2+\gamma}$ or in case (3) is proportional to the increase in drag due to the extra speed, i.e.

$$\text{work} \sim \text{drag} \sim W^{1/2+(3/2)\gamma}.$$

If in the above we also included the extra workload imposed by acceleration when fish obtain their food by sudden darts, then the values of the exponent of W would be even larger.

Of these three theoretical cases the first one, assuming no increase in either distance travelled or swimming speed, implies a special, virtually sedentary, life which may apply to fishes when the food is very abundant or behaviour highly specialized. From the latter two cases we would conclude that, regardless of the value of γ, the work output needed to acquire rations at a rate proportional to W^{γ} increases faster than W^{γ}. If the work requirement is a significant part of the total metabolism at any weight, this imposes a rather severe restriction on the ability of fish to grow much beyond this weight.

While Brett (1963) did not study the influence of body size, his experimental work demonstrated that at given size the simple hydrodynamic drag equation predicts the drag on a dead fish, but not on living fish. He suggests that it underestimates drag at low and high velocities and overestimates it

for intermediate velocities. If this be the case in nature, distance or swimming speed increases may not be such poor parallels to the mechanisms that fish actually use for increasing food consumption as is suggested by our logically simple formulation. But whatever the exact formulation, we can only conclude that the amount of food picked up by the fish is not likely to be a simple function of distance travelled or swimming speed, which accords with Ivlev's experimental observations.

This combination of theoretical and experimental information on the relation between activity, work output, and metabolic rates suggests that, with increasing size, fish obtain at least part of their increased food requirement by increasing their grazing efficiency, possibly by increasing the rate of picking up available food, possibly by increasing the size of food chunks picked up, or by being faster at catching given sized particles when an extra spurt of speed is advantageous, or by feeding for longer periods of the day. Considerations of this kind thus reveal the complexity of the food-getting processes necessary for sustained growth but do not lead to deductions specific enough to provide an unequivocal basis for a growth equation. We must therefore make further demands on experimental data for information on the actual nature of change of the ration with increasing size.

FOOD, GROWTH EFFICIENCY, AND BODY WEIGHT

It has long been known that the efficiency of the use of food for growth is high in the embryo and early larval stages of fishes and lower at later periods in their life. This efficiency, measured as $\Delta W/R\Delta t = K_1$, or $\Delta W/a'R\Delta t = K_2$ depending on whether total rations $R\Delta t$, or "assimilated" rations, $a'R\Delta t$ are used, has been termed by Ivlev (1945) the growth coefficient of the first or second order, and studied by various workers in relation to size, age, and food intake (cf. Winberg, 1962). From our review of the results of various feeding experiments (Paloheimo and Dickie, 1965b, in preparation), we have found that for a given type of food

$$\left.\begin{aligned} &\log \frac{\Delta W}{R\Delta t} = -a - bR \\ \text{or}\quad &K_1 = \frac{\Delta W}{R\Delta t} = e^{-a-bR} \\ \text{or}\quad &\frac{\Delta W}{\Delta t} = R\, e^{-a-bR} \end{aligned}\right\} \qquad (5)$$

where a and b are constants and the remaining symbols are as before. That is, for a given food type, the logarithm of the growth efficiency is linearly related to the rations. This relationship is termed here the K-line. It implies

that, beginning with a maximum value at low feeding levels, given by $\frac{\Delta W}{R\Delta t} = e^{-a}$, the growth efficiency decreases by a constant fraction, e^{-b}, for each unit increase in amount consumed per unit time, and is independent of the size of the fish. We note that the product bR is independent of the time unit used in measurement and that the maximum rate of growth occurs when $bR = 1$, at which point we find that the growth is $\frac{\Delta W_{max}}{\Delta t} = 1/be^{a+1}$.

Equation (5) is derived empirically from results of laboratory experiments on the growth and feeding of fishes, and the evidence supporting it will be discussed more fully in the paper in preparation cited above. In the short space available here we note that our review of the available data suggests that it holds for widely different levels of food supply, and that feeding rates above those giving maximum growth do occur. It also appears that the relation holds over a wide range of temperatures, provided that with temperature change the fish of different sizes are permitted to adjust the amount they will eat from a particular supply.

Changes in the caloric content of the food, or the basic energy distribution within the animal, imposed, for example, by environmental changes such as salinity, appear to affect the numerical value of a, but not of b, though assessment of the conditions under which b is stable, or will change, is a large area for further experimental study. Whatever the results of such study, it appears that from observations of growth efficiency we can obtain an expression describing the compensatory energetic balance which fish of different sizes actually do establish between their potential for greater grazing efficiency and the inevitable increase in routine and active workload.

It is a striking feature of this equation that, although the experiments dealt with fish at different sizes, the actual growth efficiency seems to be independent of body weight. That is, the same absolute ration appears to lead to the same absolute growth rate no matter what the size of fish. There are obvious restrictions, in the sense that there is an upper limit to the size of ration a particular size of fish can consume and assimilate per unit time, and a minimum ration required to meet its routine requirements. In addition, it is generally recognized that consumption of a given ration per unit time may imply certain restrictions on the food type, particularly with respect to particle size. That is, for a large fish to increase its rate of consumption beyond a given point may require a change in diet from one food type to another, which may, in turn, imply a different value of a and b. Equation (5) therefore describes growth efficiency only for a given food type and over a certain practical range of rations and body sizes. Using it for studying growth over the life-span of a fish will usually require that we consider life-history stanzas which will be related to different food types but may be defined by reference to a range of rations or body sizes. Separate growth efficiency lines of the equation (5) type may apply within each of these stanzas.

INTERACTIONS OF FOOD, METABOLISM, AND GROWTH

It was noted from experimental studies of fish metabolism under different feeding schedules that at a given availability of food the level of metabolism expressed by α remained constant. That is, from equations (2) and (3)

$$T = \alpha W^{\gamma} = R - \Delta W/\Delta t.$$

Substituting equation (5) we have

$$T = R(1 - e^{-a - bR})$$

from which it appears that the rations required for a fish of any size W to stay at a given metabolic level may be calculated from

$$\alpha W^{\gamma} = R(1 - e^{-a - bR}) \tag{6}$$

We have thus a simple expression for the metabolism at given body weight as a function of R. Although it cannot be solved explicitly for R in terms of W, corresponding sets of values can be readily calculated as is illustrated in Table I. It is apparent that, with increasing R, the term in brackets approaches 1. Hence as W increases, αW^{γ} approaches closer and closer to R. The consequence of this, also apparent from equation (5), is that growth decreases at high values of R.

Expression (6) may be used to make general deductions about growth of fishes. It gives rise to a family of growth curves depending on values taken by the parameter values for different environmental conditions, species, life-history stages, or available food types. In order to discuss its general features without being limited by its potential complexity, it is convenient to transform the parameters into terms of biologically meaningful reference points.

Standardization of Growth Curves

We note that the general level of efficiency, i.e. e^{-a}, does not change much from one species or food type to another. From our review of the literature it appears that 0.25 to 0.75 are practical limits in feeding experiments and in nature the range may very well be less than this (cf. Slobodkin, 1961). However, the coefficient, b, may take widely different values, as may R, the food intake. Their product determines the growth, and in a practical way also the maximum size the fish can attain. It is therefore convenient to refer this variable growth–rations relationship to a standard value of bR. We will take it as the point at which the maximum growth increment is obtained.

Since at maximum growth rate bR = 1, we may take as our revised scale of measurement of rations, rations in units of $1/b$. If rations on this new scale are termed r, then the product

$$bR = r.$$

Body weight at $r = 1$ is given by

$$\alpha W^{\gamma} = (1 - e^{-a-1})/b$$

which suggests that the corresponding scale for measuring weight should be

$$\left(\frac{1 - e^{-a-1}}{\alpha b}\right)^{1/\gamma}.$$

For greater simplicity, as well as to be able to study effects of changes in general feeding efficiency on growth (cf. Fig. 1), we use only the term $(1/\alpha b)^{1/\gamma}$ as a scaling factor. That is, we will continue to specify the quantity e^{-a} explicitly in the equations, and take the rescaled weight, w, as

$$w = (\alpha b)^{1/\gamma} W.$$

TABLE 1. Values of metabolic expenditure (T), growth (ΔW), and body weight (W) at different levels of total metabolism (α), corresponding to different rate of consumption of rations (R). The values of R, ΔW and T are in terms of grams wet weight per day. Estimates of a and b are from results of feeding experiments on small hatchery trout fingerlings reported by the Cortland Hatchery (Tunison *et al.*, 1939; Phillips *et al.*, 1940). The calculations assume that the food, which was a hatchery mash, had the same caloric value per unit weight as did the fish. The value of $\alpha = 0.04$ is slightly above the standard metabolic level, and 0.20 is near the maximum sustained metabolic level. Values of other constants: $e^{-a} = 0.40$; $b = 0.45$; $\gamma = 0.80$.

				W where		
R	bR	$T = \alpha W^{\gamma} = R(1 - e^{-a-bR})$	$\Delta W = R - T$	$\alpha = 0.04$	$\alpha = 0.10$	$\alpha = 0.20$
0.05	0.023	0.031	0.019	0.71	0.23	0.09
0.10	0.045	0.062	0.038	1.72	0.55	0.23
0.20	0.090	0.127	0.073	4.23	1.35	0.57
0.50	0.225	0.340	0.160	14.54	4.62	1.94
0.75	0.338	0.536	0.214	25.7	8.16	3.43
1.00	0.450	0.745	0.255	38.7	12.30	5.18
1.20	0.540	0.920	0.280	50.6	16.0	6.74
1.50	0.675	1.195	0.305	69.8	22.2	9.35
2.00	0.900	1.675	0.325	106.5	33.9	14.26
2.10	0.945	1.774	0.326	114.4	36.4	15.3
2.22	1.000	1.893	0.327	124.1	39.5	16.6
2.30	1.04	1.974	0.326	130.7	41.6	17.5
2.50	1.13	2.18	0.325	148.0	47.0	19.8
3.00	1.35	2.69	0.311	193.0	61.2	25.2
5.00	2.25	4.75	0.250	392.0	125.0	52.4
10.00	4.50	9.95	0.050	988.0	314.0	132.0

Substituting, we rewrite the weight–rations relationship of equation (6) as

$$w^{\gamma} = r(1 - e^{-a-r}) \tag{7}$$

in which general form the original rations and weight observations for the different life-history stanzas of a species or for different species are rescaled by reference to a common ecological-physiological reference point.

It is readily verified that the rescaling is in the correct units. That is, from the original growth efficiency equation (5)

$$\log \frac{\Delta W}{R\Delta t} = -a - bR$$

we infer that b has the dimension time/weight of rations (or time/calories, depending on the units of R and W), hence that the product bR is independent of time.

From the identity

$$\alpha W^{\gamma} = (\alpha^{1/\gamma} W)^{\gamma}$$

α has the dimension (weight)$^{1-\gamma}$/time. Hence the weight scaling factor $(\alpha b)^{1/\gamma}$ has the dimension 1/weight as it must.

The import of the rescaling in terms of physiological and ecological characteristics emerges more explicitly from consideration of the time units. In the original energy equation, we wrote

$$\frac{\Delta W}{\Delta t} = R - T = R - \alpha W^{\gamma} \tag{4}$$

in which the rates were measured over some unit period. For our rescaling we rewrite equation (4) as

$$\frac{(\alpha b)^{1/\gamma}\Delta W}{b^{-1}(\alpha b)^{1/\gamma}\Delta t} = \frac{\Delta w}{b^{-1}(\alpha b)^{1/\gamma}\Delta t} = r - w^{\gamma} \tag{8}$$

The equation in this form shows that, if rations are measured in units of $1/b$ and weight in units $1/(\alpha b)^{1/\gamma}$, time is measured in units $b/(\alpha b)^{1/\gamma}$. For simplicity we write (8) as

$$\frac{\Delta w}{\Delta t} = r - w^{\gamma} \tag{9}$$

where t is now measured in units of $b/(\alpha b)^{1/\gamma}$. It is readily verified that this ratio of rations and weight scaling factors does in fact have a dimension of time and is independent of the original units of measurement.

From the foregoing it is evident that in the rescaled form time is in units which are proportional to the rate of total metabolic expenditures of the fish

under observed conditions. That is, the rescaling brings the various curves describing sets of experimental observations to a common curve based on the rates of physiological processes underlying growth.

There is, of course, the possibly important situation in which this scaling breaks down, when b, the slope of the K-line (Equation (5)), is zero. That is, if growth efficiency does not change, the reference point, where fish attain their maximum growth, is pushed to infinity. More specifically, for a fish which stays on a fixed T-line (i.e. equation (3) with constant α), we have when $b = 0$

$$\left.\begin{aligned} T &= \alpha W^{\gamma} = R(1 - e^{-a}) \\ \Delta W &= Re^{-a}\Delta t = cW^{\gamma}\Delta t \end{aligned}\right\} \tag{10}$$

where $c = \alpha e^{-a}/1{-}e^{-a}$. The latter equation in (10) may be integrated, giving the weight (or growth) as a function of time, thus:

$$W = \left((1 - \gamma)\ c\ (t - t_0) + W_0^{1-\gamma} \right)^{\frac{1}{1-\gamma}} \tag{11}$$

With growth of the form suggested by equation (11), in which there is no maximum growth to use as a biological reference point, it would appear that for given γ the only possible differences in underlying mechanism which could give rise to various growth patterns would be the different metabolic levels at which the fish operate. Since this implies changes in the basic metabolic turnover, it would thus appear appropriate to scale the time axis in units proportional to α, or to be more specific in units of $(c/W_0)^{1/1-\gamma}$. Reference to equations (10) and (11) shows that this would reduce the different growth patterns to a common curve expressed by the equation

$$w = w_0 \left((1 - \gamma)\ (t - t_0) + 1 \right)^{\frac{1}{1-\gamma}} \tag{12}$$

where, although the notation has not been changed, t and t_0 are expressed in the new time scale. For a value of $\gamma = 0.8$, equations (11) and (12), which arise when $b = 0$, show that the body weight W increases as the 5th power of time. Such a rate of growth is fast enough to be indistinguishable from exponential growth over a limited range of W or t.

FOOD, GROWTH, AND GROWTH EQUATIONS

Our rescaling of parameters permits us to discuss the relations between rations and growth in general terms. Beginning with the case where growth efficiency decreases with increase in rations consumed ($b>0$) we may construct curves of rations consumed per body weight, as expressed by equation (7). These are plotted in Fig. 1 for two values of the maximum efficiency, e^{-a}. In curve A, $e^{-a} = 0.4$; in curve B, $e^{-a} = 0.6$. We also show two reference

lines, the straight line where $r = w$ and the curve where $r = w^{\gamma}$. It appears that curves A and B are rather close to one another, and that both approach the curve $r = w^{\gamma}$ at higher values of body weight. It can be shown that in this formulation rations assimilated per unit time, as a function of body weight, increase faster than w^{γ} up to a point where maximum growth occurs, i.e. $r = 1$, then slow down, approaching gradually the $r = w^{\gamma}$ curve.

Also plotted in Fig. 1 are the growth increments per given ration — curve C. These growth increments may be used to construct the growth curve as a function of time. That is, from equations (5) and (9) growth is determined analytically by a system of two equations:

$$\left.\begin{aligned} w^{\gamma} &= r(1 - e^{-a-r}) \\ \Delta w &= r\, e^{-a-r}\Delta t \end{aligned}\right\} \qquad (13)$$

The second equation may be written as the differential equation

$$\frac{\Delta w}{\Delta t} = r\, e^{-a-r} \qquad (14)$$

in which the ration r is a function of body weight defined by the first equation in (13). Equation (14) must be solved numerically, its solution being presented in graphic form (solid lines) in Fig. 2, using three different time scales.

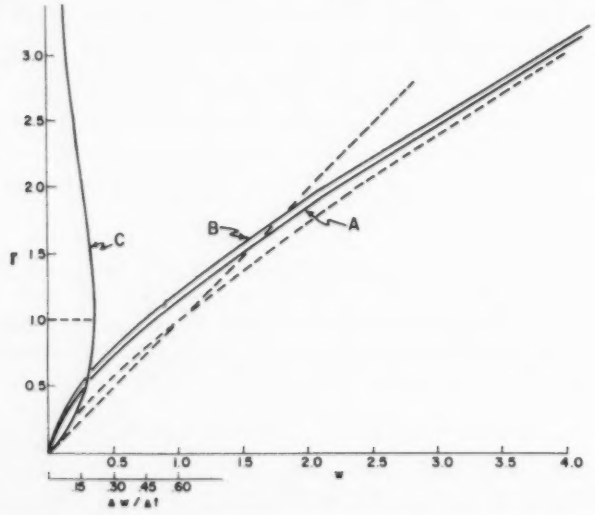


FIG. 1. Relation between rations, r, body weight, w, and growth, $\Delta w/\Delta t$. Curves A and B are for $w^{\gamma} = r(1-e^{-a-r})$ where $e^{-a} = 0.4$ (Curve A) and $e^{-a} = 0.6$ (Curve B). Curve C is for $\Delta w/\Delta t = re^{-a-r}$ where $e^{-a} = 0.6$. The dotted reference curves show $r = w$ and $r = w^{\gamma}$, where $\gamma = 0.8$. Maximum growth rate occurs at $r = 1.0$, by definition.

In calculating the solution we have made use of the identity

$$\frac{dw}{dt} = \frac{dw}{dr}\,\frac{dr}{dt} = r\,e^{-a-r}$$

where from (13)

$$\frac{dw}{dr} = \frac{1}{\gamma}\left(r(1-e^{-a-r})\right)^{(1/\gamma)-1}\left(1+e^{-a-r}\,(r-1)\right) \tag{15}$$

When these two equations are substituted in (14) we get a differential equation in terms of r and t of the form

$$\frac{dr}{dt} = \frac{\gamma r}{\left(r(1-e^{-a-r})\right)^{(1/\gamma)-1}\,(e^{a+r}+r-1)} \tag{16}$$

which, by use of a computer, may be readily integrated to give t in terms of r. The corresponding values of w are then obtained from the first equation in (13).

For comparison we may approximate the food intake in (13) by the reference curve of Fig. 1, where

$$r = w^{\gamma}.$$

This leads to the differential equation[2]

$$\frac{dw}{dt} = w^{\gamma}\exp\,(-a-w^{\gamma}) \tag{17}$$

which may be integrated to give

$$\int_{w_0}^{w}\left(\exp\,(w^{\gamma})\right)w^{\gamma}\,dw = e^{-a}(t-t_0).$$

The resulting curves, using the same three time scales, have been plotted in Fig. 2 (dotted lines) for comparison with the numerical solutions of the more exact case. The simpler approximate form may frequently be useful in preliminary explorations of food–growth data.

The growth curves of Fig. 2 are characterized by an inflection in the early growth stages, thence a period of relatively rapid growth followed by a slowing down. In terms of a finite life-span, this slowing down may appear as a virtual growth stoppage, but, except for this, the curves do not have a the-

[2] $\exp\,(x) = e^{x}$.

oretical asymptote. That is, the curves suggest that body weight continues to increase throughout the fish's life and would theoretically reach infinity in infinite time.

The rate at which fish go through the phase of rapid growth is related to our time scaling: $1/\alpha^{1/\gamma}\, b^{(1/\gamma)-1}$. It is apparent that as the values of α and b are increased, the time units become shorter; that is, larger values of α and b mean that in solar time units the fish go through the period of rapid growth more quickly, and reach the region of slow growth that much sooner.

It will be noted that, for a given proportional change in their numerical values, α has a much greater effect on the time scale than does b. However, reference to the original definitions of these constants in equations (3), (5), and (6), shows that, in fact, their potential ranges of values are very different. Investigations by a number of authors suggest that the metabolic level, expressed by α, varies from a given base level for maintenance metabolism to a maximum sustained or active metabolic level of the order of only five to ten times higher. On the other hand, b, expressing the slope of the K-line, is potentially capable of much greater relative variation. We have no experimental or theoretical data to show what its limits are. As noted on page 526 and as written in equation (5), growth–feeding experiments suggest that it is greater than zero and has a negative sign, but its upper limit may include rather large absolute values. Its lower limit almost certainly includes the case where $b = 0$, a situation which we consider in more detail below. In special cases it may even appear to take negative values (i.e. the K-line has a positive slope), although this must be an exceptional situation.

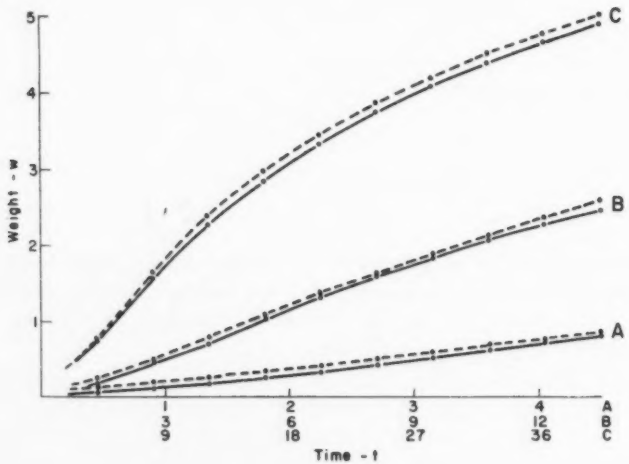


FIG. 2. Growth curves for fish from equation (13) — solid lines, and equation (17) — broken lines, using three time scales.

The Parker-Larkin Equation

It was pointed out above that in the case where $b = 0$, our time scale might well be measured in terms of α. In this situation growth increases steadily with time at a rate which closely simulates exponential growth. The growth equation in original units was given in (11), and with the time scale in units of α in equation (12).

Equation (11) is identical with that given by Parker and Larkin (1959) and found by them and others to describe the growth of a number of species through various life-history stanzas. They arrive at this type of growth curve starting from the basic equation

$$\frac{dW}{dt} = kW^x$$

which upon integration gives

$$W^{(1-x)} = (1-x)\ k\ (t-t_0) + W_0^{(1-x)}.$$

They fit the curve to data by choosing that value of x which minimizes residual error. Their exponent x is obviously equivalent to γ in equation (11).

It is of no little interest in comparing our respective formulations that, in fitting their growth curve to data for two species of salmonids, Parker and Larkin found that the freshwater phase of steelhead (*Salmo gairdneri*) growth was best described by a value of $x = 0.8$. In terms of our equations this suggests that $\gamma = 0.8$, and the K-line has a slope $b = 0$ while the T-line has a constant value of α (cf. equation (10)).

On the other hand, Parker and Larkin note that they generally found values of x which were less than 0.8, the range they encountered being from 0.83 to 0.50. It should be noted in this connection that a good fit to an equation of the form $W^{1-x} = kt + W_0^{1-x}$ to growth data over the limited range to which it is likely to apply does not necessarily imply that the underlying mechanism is of a $dW/dt = kW^x$ type. Thus values of $x \neq 0.8$ do not necessarily imply that $\gamma \neq 0.8$. The experimental evidence suggests in fact that γ may be rather stable. Our formulations therefore suggest that for values of $x < 0.8$, γ remains constant while growth efficiency $b > 0$ (decreases with rations increase) and possibly that there are changes in α.

Parker and Larkin found that the marine phase of growth of steelhead was characterized by $x = 0.7$, and of the chinook salmon (*Oncorhynchus tshawytscha*) by $x = 0.6$. Since it is known that change from fresh to salt water is accompanied by profound physiological changes (cf. Alderdice, 1963) this change in growth pattern is hardly unexpected. In our terms it could be interpreted as a progressive relative decrease in α during the marine phase, or, alternatively, a lower, though constant α, but with $b > 0$ in the new marine growth stanza. The applicability of any such interpretation requires checking the metabolic levels by field observations.

In a more recent paper, Larkin and Ayyangar (1961) found values of x lower than 0.8 for three species of fish and for older sea scallops (pelecypod molluscs: *Placopecten magellanicus*). Cooper (1961) also found lower than 0.8 values for strains of hatchery-reared brook trout. These scattered data confirm the expectation from general observations of decreasing growth rate with age that low values of x may be the rule rather than the exception. That is, in general, we may expect that where α is constant, $b > 0$.

The von Bertalanffy Equation

Given the apparently general case of a K-line having a negative slope (i.e. $b > 0$), we have still to consider the characteristic of fish growth suggested by our formulations, that the growth does not have a theoretical asymptote. Since fish have a finite life-span, this is perhaps not as perplexing as first appears. Indeed it may well be a simple property of the statistical fittings. However, it is illustrative to consider in this connection the commonly used von Bertalanffy growth equation which assumes asymptotic growth.

The von Bertalanffy growth curve is graduated by a differential equation which may be written in the form

$$\frac{dW}{dt} = 3H(W_t^{2/3} W_\infty^{1/3} - W_t) \qquad (18)$$

where W_∞ is the assumed final (asymtotic) size and the values of the coefficients and exponents are assigned by consideration of possible surface–volume metabolic relations. From this equation it is obvious that where $W_t = W_\infty$ the growth rate = 0 and algebraically the fish is incapable of further growth. Using our growth curves of Fig. 2, we have plotted in Fig. 3 the length of fish (i.e. $W^{1/3}$) at time t against the weight at time $t + 1$, as separate "Walford" lines, for each of the three time scales. The early phase of growth gives reasonably good fits to a straight line intersecting the 45° diagonal, as is implied by the von Bertalanffy growth curve. However, inclusion of the points for later growth introduces considerable curvature; in fact, the estimate of the intercept, W_∞, may well depend upon how many of the older fish are included in the population growth sample.

In many cases the von Bertalanffy growth curve is fitted to data consisting mainly of young fish well below the projected final size. Hence the value of W_∞ apparently reflects the early growth. In view of the fact that the growth of different species has often been characterized by reference to W_∞ (Beverton and Holt, 1959; Holt, 1962), it may be worth while drawing attention to the relationship between the estimated W_∞ and our growth scaling.

We may consider data for young fish when the fit to the von Bertalanffy equation is such that estimates of W_∞ may be used to predict the inflection point of the growth curve. Differentiation of (18) shows that this inflection

point occurs at $W_t = 8W_\infty/27$. If we equate this inflection point with that predicted by the growth relations suggested here, we have

$$\frac{8}{27} W_\infty = \left(\frac{1 - e^{-a-1}}{\alpha b} \right)^{1/\gamma}.$$

That is, W_∞ is proportional to our physiological time scale (see p. 529).

The cases where asymptotic growth is confirmed by the data are rather rare, due possibly to inadequate sampling. On the other hand, some species show a tendency for curvatures of the sort illustrated in Fig. 3 (cf. Ricker, 1958, pp. 195–197), indicating that asymptotic growth is not a universal phenomenon among fishes. An apparent asymptote could be construed as a manifestation of the older fish having gotten to a region on the K-line where the growth efficiency is close to 0 as a consequence of their having failed to evolve a new ecological niche. The presence of a genuine asymptote would suggest that one or more of the three following conditions are met:

a) Fish do not stay on a fixed T-line, but at larger sizes gradually reduce their metabolic level (α in equation (3)) towards the maintenance level.
b) The K-line (growth efficiency) is curved downward at larger R. (Note that a steep slope will give the appearance of an imminent growth stoppage but not a theoretical asymptote.)

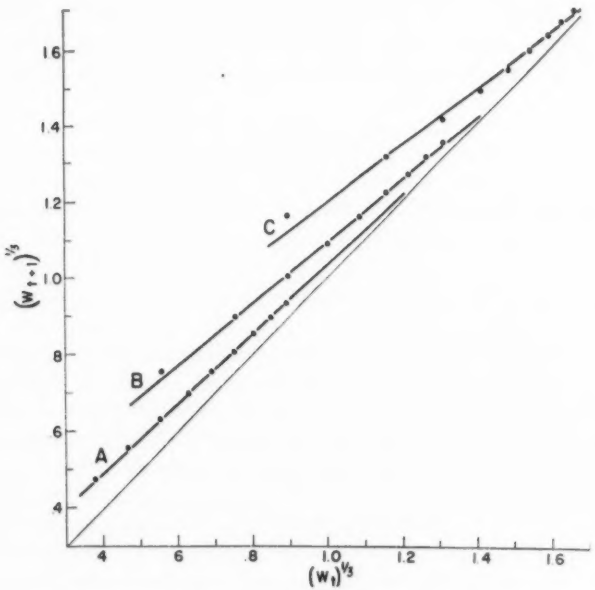


FIG. 3. Walford plots of the growth curves of Fig. 2.

c) When the growth curve is an average for a population, rather than the growth of one individual, the asymptote could have been produced by an interaction between rates of growth and mortality, the faster-growing fish having the higher mortality. In fact, the apparently asymptotic nature of growth of a number of species is less marked if growth rates are plotted using back-calculated lengths for individuals (Parker and Larkin, 1959).

Further speculation about the nature of growth in fishes should perhaps be restrained until further experimental data are available. An advantage of the type of formulation suggested here is that, while studies of growth require the statistical fittings of actual growth data, the understanding of variations in the basic pattern, and the mechanisms which give rise to them may be supplemented by studies of the metabolic rates of the sort reported by Fry (1957) and his associates from the laboratory, and by Wohlschlag and Juliano (1959) from the field, as well as food–growth relations of the sort suggested by Ivlev (1945), Winberg (1962), and Paloheimo and Dickie (1965a, b in preparation). Such information would appear essential in understanding the generality of biological phenomena and their consequences for population production processes.

DISCUSSION

It is unlikely that the growth of many species of fish can be graduated over their entire life-spans by a single simple growth model of the type suggested here, necessitating a breakdown into different life-history phases and separate assessment of the role of each in overall production. This is an obviously complex process, but consideration of food–growth relations at even the simple level reveals consequences of importance to the understanding of a natural biological community.

We note first of all that our attempt at specification of growth in terms of metabolic levels and growth efficiencies implies that one should be able to reverse the investigation process. That is, given observations of the growth rates and general knowledge of metabolism and growth efficiency, it should be possible to deduce the general level of feeding. Such information would be valuable as a tool in specifying the relative success of grazing of the different sizes of the same species, or of different species components of the community.

In the second place, the factors contributing to changes in growth rates of fishes in terms of their mechanism for counteracting the increasing workload with size, or work output efficiency, have been extensively studied in recent years (Fry, 1957; Bainbridge, 1961; Brett, 1962). However, as concluded above, our knowledge about how these active metabolic components are related to acquiring food, i.e. to the grazing efficiency, is still too limited to permit a choice among reasonable alternatives to explain growth mechanisms and construct growth curves. Where possible we have attempted to use experimental results of studies of metabolism and growth efficiency to suggest what kinds of adjustments the fish actually do make. These appear to be

capable of relatively simpler expression than might have been anticipated, and suggest further experiments on food, growth, and activity in relation to the T- and K-lines (equations (3) and (5)) which could throw light on the adaptive significance of various behaviour patterns and the anatomical modifications for different types of swimming.

Ramifications of these two aspects of growth are of sufficient importance for discussion in a separate paper. In what follows here we confine attention to certain consequences of food–growth relations which have a direct bearing on management of exploited fish stocks.

For purposes of exposition we will assume that there is only one growth phase which describes growth of the exploited sizes in a fish stock. That is, we consider that the growth of these exploited sizes at any time can be described by reference to a single T-line (equation (3)) and single K-line (equations (5) and (7)). Within this stock we further consider only two of the size-groups of the fish chosen so that, in growing from one to the other, the total growth is just balanced by mortality so that the biomasses of the two groups are equal. If we put the average size of the smaller fish as equal to w, and the average size of the larger as W, then under the specified conditions the number of small fish in the stock will be proportional to W, the number of large proportional to w, and the biomasses proportional to $Ww = wW$. Since both groups are feeding on the same food supply, the individuals are "operating" on the same T-line. Therefore the rations per individual fish may be deduced from the relationship $w^{\gamma} = r(1 - e^{-a-r})$ — equation (7) — or approximately by $w^{\gamma} = r$. We observe then, that the amount of food consumed by the group of smaller fish is proportional to Ww^{γ}, while the amount eaten by the group of larger fish is proportional to wW^{γ}. But for all $\gamma < 1.0$ we have

$$Ww^{\gamma} > wW^{\gamma}.$$

It thus appears that the two size-groups do not take equal proportions of the food; rather, that per unit biomass, the group of smaller fish is taking the larger proportion of the consumed food.

Put in other terms, the above inequality implies that, if the food supply is constant, removal of a given weight of small fish from such a balanced stock would permit their replacement by a greater than equal weight of large fish. In yet other terms, we conclude that the cost, in terms of use of energy units in the system, of maintaining a given weight of large fish, is less than the cost of maintaining the same weight of small ones. Given such a conclusion, it would appear that there may be some evolutionary advantages for a species in the attainment of large average body size. That is, in situations of periodic or chronic food shortage, larger animals not only have lower metabolism per unit weight, hence larger storage per individual, which provides resistance to starvation, but can be more readily supported by minor amelioration of the feeding conditions per unit biomass.

In considering the long-term production available as yield from the exploitation of such a stock of fish, the growth efficiency rather than relative maintenance cost is the feature of direct relevance. That is, in terms of sustained yield which could be taken by man, we are interested not so much in the biomass present as in the proportion of the food energy supply which can be continuously cropped as fish flesh. If, in the first instance, we suppose that the slope of the K-line (growth efficiency) is 0, then equal rations for the different size-groups result in equal growth production. Thus, in our hypothetical example, the sustainable yield of the smaller size-group is greater than that from the large in the ratio $Ww^{\gamma}/w\mathrm{W}^{\gamma}$. If, as seems to be the more general case, the slope of the K-line $b \neq 0$, then from equations (5) and (7) the use of food of the small fish Ww^{γ} for growth is approximately proportional to $Ww^{\gamma} \exp(-w^{\gamma})$ and of the large to $w\mathrm{W}^{\gamma} \exp(-\mathrm{W}^{\gamma})$. That is, the simple ratio above is increased by a fraction proportional to $\exp(-w^{\gamma} + \mathrm{W}^{\gamma})$. We conclude that within a life-history stanza a given food abundance leads to a higher production of replaceable fish flesh if the producing population consists of the smaller more efficient fish than if it consists of the larger fish.

Stated in these terms, our conclusions appear rather obvious and in agreement with recognized, if implicit, ecological principles, although they do not appear to have been accepted in much of the theory guiding current fisheries management. Thus yield-per-recruit models widely used as theoretical background for current fisheries management postulate that, given a constant average number of fish recruited to an exploited stock, the objective of management is to crop them on the average at that size when, through the balance of growth and mortality, they have attained maximum biomass. This system calls for increased age, hence size, at first capture as rate of exploitation is increased. However, such formulations neglect the possibility that the food energy released by the cropping is itself available to other components of the community. That it is in fact used by the community is again an implicit principle in ecology and has been demonstrated, among others, by the finding of Odum and Smalley (1959) that community energy flow is homeostatic. In view of our conclusion that a given biomass of small animals not only may obtain a more than proportional share of food, but uses it more efficiently for growth, one would rather suppose that, *ceteris paribus*, the objective of management for maximum long-term sustained production should often be the maintenance of a population of fish of as small an average size as it is practicable to harvest and handle.

It will be obvious to anyone having knowledge of the complexity of organization and food-chains in a natural community that it is not a simple matter to predict the effects of alteration of an established order. Thus, exploitation of any one size-group or life phase of a species does not mean that compensatory changes in community production will be reflected through other structural elements of the same species or even in harvestable components of other species. This has been well illustrated in at least one case by Moiseev's (1946) account of changes in the relative species composition of

flatfishes in the Gulf of Peter the Great, following initiation of an intense fishery. Similar species composition changes are recognized but less well documented in areas such as the Great Lakes of North America, the North Sea, and the East China Sea, although explanations for them are not so directly apparent because of the long time-trends confounded with physical environmental changes. From considerations of the mechanisms which underlie the food–growth relations, it would appear that replacements will ultimately depend not only on the food requirements for sustaining a given T-line, and the output in terms of growth, but the opportunities for satisfying a given food requirement and the ways in which fish take advantage of them in a competitive situation.

At the moment there is a need for a combination of laboratory experiments and field observations to show how changes in feeding opportunities and grazing efficiencies are reflected in the K-lines and T-lines. Results of such studies may go far toward increasing our understanding of natural production processes, even if not to predict them. In any case, the results may have great significance for the understanding of the interaction between different types of exploitation and the processes underlying natural production.

ACKNOWLEDGMENTS

We wish to express our thanks to Dr J. L. Hart, Director of the Biological Station, St. Andrews, N. B., for his sustained interest and support of this work. This paper is largely based on work carried on in facilities provided by the Department of Zoology of the University of Toronto. We gratefully acknowledge the kindnesses of Dr K. C. Fisher, Chairman of the Department of Zoology, and of Dr G. B. Langford, Chairman of the Great Lakes Institute, who made this arrangement possible.

We have been stimulated during this work by discussions of our general approaches and methods with Dr A. G. Huntsman. It is a privilege to present our contribution to the theme of fish-environment interactions, which he has played on a wider scale, in this volume published in his honour.

REFERENCES

ALDERDICE, D. F. MS, 1963. Some effects of simultaneous variation in salinity, temperature and dissolved oxygen on the resistance of juvenile coho salmon (*Oncorhynchus kisutch*) to a toxic substance. Ph.D. thesis, Department of Zoology, University of Toronto.

BAINBRIDGE, RICHARD. 1961. Problems of fish locomotion. *Symposia Zool. Soc. London*' No. 5, pp. 13–32.

BERTALANFFY, L. VON. 1938. A quantitative theory of organic growth. *Human Biology*, **10**(2): 181–213.

1957. Quantitative laws in metabolism and growth. *Quart. Rev. Biol.*, **32**(3): 217–231.

BEVERTON, R. J. H., AND S. J. HOLT. 1957. On the dynamics of exploited fish populations. *U. K. Min. Agric. and Fisheries, Fish. Invest.*, Ser. 2, Vol. 19, 533 pp.

1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. CIBA Foundation Colloquia on Ageing, **5**: 142–180.

BRETT, J. R. 1962. Some considerations in the study of respiratory metabolism in fish, particularly salmon. *J. Fish. Res. Bd. Canada*, **19**(6): 1025–1038.

1963. The energy required for swimming by young sockeye salmon with a comparison of the drag force on a dead fish. *Trans. Royal Soc. Canada*, Ser. IV, **1**: 441–457.

COOPER, E. L. 1961. Growth of wild and hatchery strains of brook trout. *Trans. Amer. Fish Soc.*, **90**: 424–438.

FRY, F. E. J. 1957. The aquatic respiration of fish. *In* M. E. Brown [ed.]. The physiology of fishes, Vol. I. Academic Press, New York, 447 pp.

HOLT, S. J. 1962. The application of comparative population studies to fisheries biology — an exploration, pp. 51–71. *In* LeCren, E. D. and M. W. Holdgate [ed.]. The exploitation of natural animal populations. Blackwell Scientific Publ., Oxford, 399 pp.

IVLEV, V. S. 1944. [The time of hunting and the path followed by the predator in relation to the density of the prey populations.] *Zool. Zhurn.*, **23**(4): 139–145.

1945. [The biological productivity of waters.] *Uspekhi Sovremennoi Biol.*, **19**(1): 98–120. [Fish. Res. Bd. Canada, Trans. Ser. No. 394]

1955. [Experimental ecology of nutrition of fishes.] Pishchepromizdat, Moscow. [Trans. D. Scott, Yale University Press, New Haven, 1961]

1961. [On the utilization of food by plankton-eating fishes.] *Trudy Sevastopolskoi Biol. Sta.*, **14**: 188–201. [Fish. Res. Bd. Canada, Trans. Ser. No. 447]

JOB, S. V. 1955. The oxygen consumption of *Salvelinus fontinalis*. *Univ. Toronto Studies, Biol. Ser.*, No. 61; *Publ. Ontario Fish. Res. Lab.*, No. 73, 39 pp.

LARKIN, P. A., AND K. V. AYYANGAR. 1961. Applications of the Parker equation to growth of aquatic organisms. *Proc. 11th Alaskan Sci. Conf.* 1961, pp. 103–124.

MOISEEV, P. A. 1946. [Information on the effect of the fishery on the condition and composition of the stock of flatfishes in the Gulf of Peter the Great.] *Zool. Zhurn.*, **25**(5): 451–457. [Fish. Res. Bd. Canada, Trans. Ser. No. 98]

ODUM, E. P., AND A. E. SMALLEY. 1959. Comparison of population energy flow of a herbivorous and a deposit-feeding invertebrate in a salt marsh ecosystem. *Proc. Nat. Acad. Sci.*, **45**(4): 617–622.

PALOHEIMO, J. E., AND L. M. DICKIE. 1965a. Food and growth of fishes. II. Effects of food and temperature on the relations between body size and metabolism. J. Fish. Res. Bd. Canada. (In preparation)

1965b. Food and growth of fishes. III. Relations among food, body size and growth efficiency. *Ibid.* (In preparation)

PARKER, R. R., AND P. A. LARKIN. 1959. A concept of growth in fishes. *J. Fish. Res. Bd. Canada*, **16**(5): 721–745.

PHILLIPS, A. M., A. V. TUNISON, A. H. FENN, C. R. MITCHELL, AND C. M. MCCAY. 1940. The nutrition of trout. *Cortland Hatchery, Rept.* No. 9 for 1940.

RICHARDS, F. J. 1959. A flexible growth function for empirical use. *J. Exp. Botany*, **10**(29): 290–300.

RICKER, W. E. 1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Bd. Canada*, No. 119, 300 pp.

SLOBODKIN, L. B. 1961. Preliminary ideas for a predictive theory of ecology. *Amer. Nat.*, **95**(882): 147–155.

TUNISON, A. V., A. M. PHILLIPS, C. M. MCCAY, C. R. MITCHELL, AND E. O. RODGERS. 1939. The nutrition of trout. *Cortland Hatchery, Rept.* No. 8 for 1939.

WEISS, PAUL, AND J. L. KAVANAU. 1957. A model of growth and growth control in mathematical terms. *J. Gen. Physiol.*, **41**(1): 1–47.

WINBERG, G. G. 1956. [Rate of metabolism and food requirements of fishes.] Nauchnye Trudy Belorusskogo Gosudarstvennogo Universiteta imeni V.I. Lenina, Minsk, 253 pp. [Fish. Res. Bd. Canada, Trans. Ser. No. 194]

1962. [The energy principle in studying food associations and the productivity of ecological systems.] *Zool. Zhurn.*, **41**(11): 1618–1630. [Fish. Res. Bd. Canada, Trans. Ser. No. 433]

WOHLSCHLAG, D. E., AND R. O. JULIANO. 1959. Seasonal changes in bluegill metabolism. *Limnol. Oceanog.*, **4**(2): 195–209.

Zooplankton from the Arctic Ocean and Adjacent Canadian Waters[1]

By E. H. Grainger

Fisheries Research Board of Canada
Arctic Biological Station, Ste. Anne de Bellevue, Que.

ABSTRACT

Zooplankton collections from the Arctic Ocean, the Beaufort Sea, and northwestern Canadian coastal waters are described, along with physical characteristics of the waters sampled. About 50 species are included.

The collections are compared with records from the central Arctic Ocean and other waters adjacent to the present region. The species are shown to fall into three groups. One is characteristic of the surface water of the Arctic Ocean, one of the Atlantic water and to a lesser extent the deep layer of the surface water of the Arctic Ocean, and one of the shallow peripheral seas of the Arctic Ocean.

The surface water group includes eight species which account for more than 95% of the copepod individuals found in the surface layer, and which appear to be the only copepods which breed in the surface layer of the central Arctic Ocean. The same species are the major constituents of the zooplankton found in the waters of the Canadian arctic, from the Arctic Ocean to Davis Strait. The deeper Atlantic species of the Arctic Ocean, more numerous as species but far less numerous as individuals than those of the surface water, occur only very rarely in the surface layers, show no evidence of breeding there, and appear to be almost entirely absent from Canadian archipelago waters inside the shelf. Clear continuity of the Arctic Ocean surface fauna through the waters of the Canadian arctic is shown, along with the almost total exclusion from archipelago waters of the deeper Atlantic fauna. This intrusion of Atlantic species into the waters of arctic Canada appears to be almost entirely restricted to the southeast part of the region, especially Hudson Strait and adjacent waters.

Development rates of two copepods in the Arctic Ocean, *Microcalanus pygmaeus* and *Calanus glacialis*, are discussed.

INTRODUCTION

This work is based primarily upon zooplankton collections made from the M.V. *Cancolim II* in the southeast Beaufort Sea and Amundsen Gulf in 1951, from Ice Island T-3 off the northwestern Canadian islands in the Arctic Ocean in 1958, from the M.V. *Salvelinus* along the Yukon and Mackenzie coasts between 1960 and 1962, and from oceanographic stations of the Polar Continental Shelf Project over the north Canadian shelf in 1960 and 1961.

Locations of stations are shown in Fig. 1. Collecting methods varied. Most of the tows were vertical, made with No. 5 and No. 6 mesh nets (apertures about 0.28 and 0.24 mm), except for those from T-3 which were done with No. 10 mesh nets (apertures about 0.16 mm). A few vertical hauls were made using No. 18 and No. 20 mesh nets (apertures about 0.08 mm). Horizontal tows were made at a number of stations, often in conjunction with

[1]Received for publication September 10, 1964.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

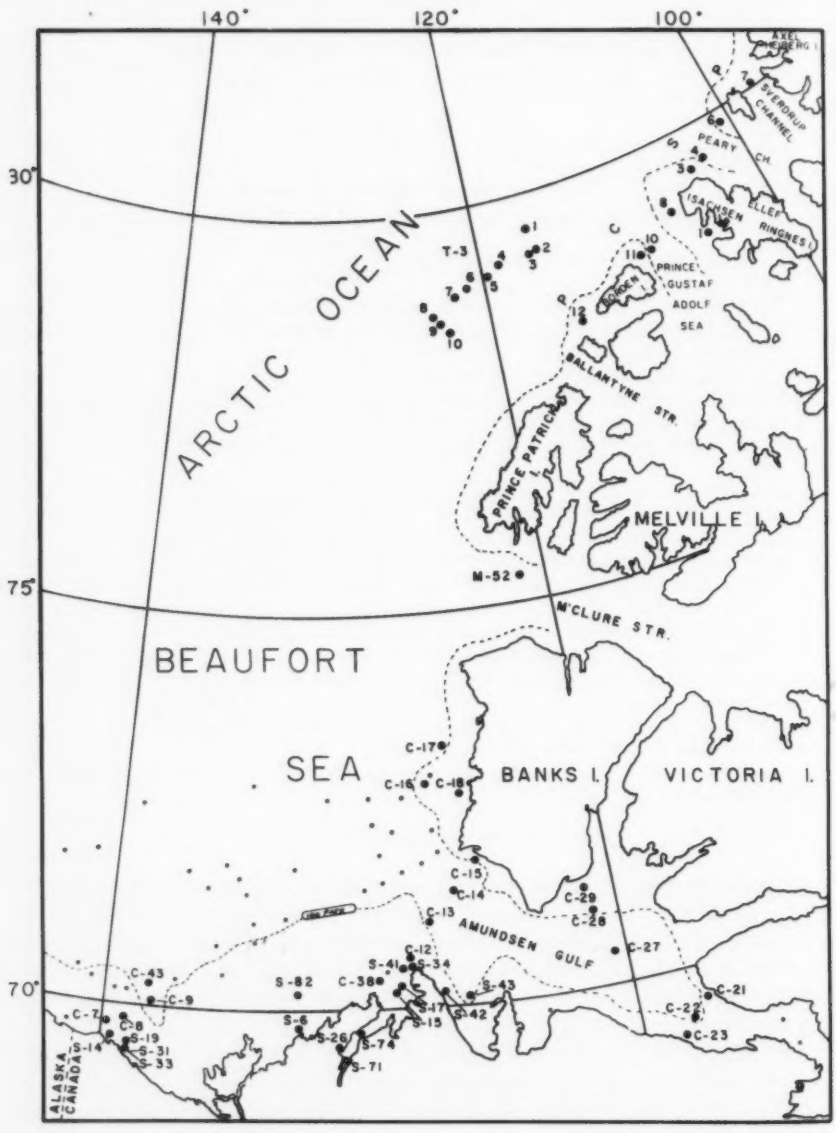


FIG. 1. Station positions. *Cancolim II* stations are indicated by the prefix "C", *Salvelinus* stations by "S", Ice Island stations by "T-3", and Polar Continental Shelf Project stations by "P.C.S.P.". Station M-52 was occupied by the ice breaker *John A. MacDonald* in 1962, the Isachsen station by the author in 1961. Small circles show positions of *Burton Island* and Canadian Arctic Expedition plankton stations.

vertical collections. Net meshes were the same as above, with the addition of No. 2 (apertures about 0.37 mm) used at station C-43. It is obvious, from the range of collecting methods used, that qualitative features only can be assessed.

Previous work on zooplankton from the region shown in Fig. 1 is described in publications from the Canadian Arctic Expedition of 1913–18 (Schmitt, 191 ; Bigelow, 1920; Shoemaker, 1920; Willey, 1920; Dall, 1925) and from the *Burton Island* cruises of 1950 and 1951 (Johnson, 1956; Hand and Kan, 1961). Zooplankton collections made in the central Arctic Ocean from the *Fram*, *Nautilus*, and *Sedov* have been reported, respectively, by Sars (1900), Hardy (1936), and Bogorov (1946), from the Russian drifting station NP 2 by Brodsky and Nitikin (1955) and from Ice Island T-3 between 1952 and 1955 by Mohr (1959), Knox (1959), and Barnard (1959). Central Arctic Ocean copepod collections have been described by Grice (1962) from the U.S. submarine *Seadragon*, and by Johnson (1963a) from the drifting station Alpha. From coastal waters adjacent to the present region, in addition to the C. A. E. and *Burton Island* material, Johnson (1953, 1958) has considered the nearshore zooplankton of the Chukchi Sea, Jaschnov (1946) the neritic waters from the Kara to the Beaufort Seas. These works provide the total of our knowledge of the zooplankton composition of the central Arctic Ocean and adjacent coastal waters of northwest North America, and it is in part with relation to these that the present material is considered here.

HYDROGRAPHY

At the inshore and shallow plankton stations along the southern edge of the Beaufort Sea (Fig. 2, 3) summer surface temperatures were high (to at least 9°C). Zero temperatures were found generally between about 5 and 10 m, below which temperatures were usually less than 0°C. At the same stations salinity at the surface in summer was usually less than 10‰, at 5 m about 20‰, and below about 10 m higher than 30‰. In southern Liverpool Bay the surface temperature was as high as 12°C, and positive temperatures were frequently found to the bottom. Bottom salinity rarely exceeded 18‰. At offshore stations in the Beaufort Sea and in Amundsen Gulf surface temperatures were lower (near zero) and surface salinities higher (more than 20 to nearly 32‰).

At the T-3 stations (Collin, 1959) temperatures at the surface were close to 0°C, and between about 10 and 50 m were as low as −1.7°C. Still deeper, temperatures increased to 0°C at about 270 m. Between 270 and 1000 m, maxima of 0.4 and 0.5°C were found, and below about 1000 m temperatures were again negative. Salinity values, often less than 1‰ in the upper 1 or 2 m, reached 34‰ at around 200 m and about 34.9‰ at 1000 m. At the Polar Continental Shelf Project stations and in M'Clure Strait temperature and salinity features were similar to those of the Arctic Ocean (Collin, 1963), except for seasonal differences in the upper few metres associated with different periods of plankton collecting. The Isachsen curves run very close to the upper parts of those of T-3 with respect to both temperature and salinity.

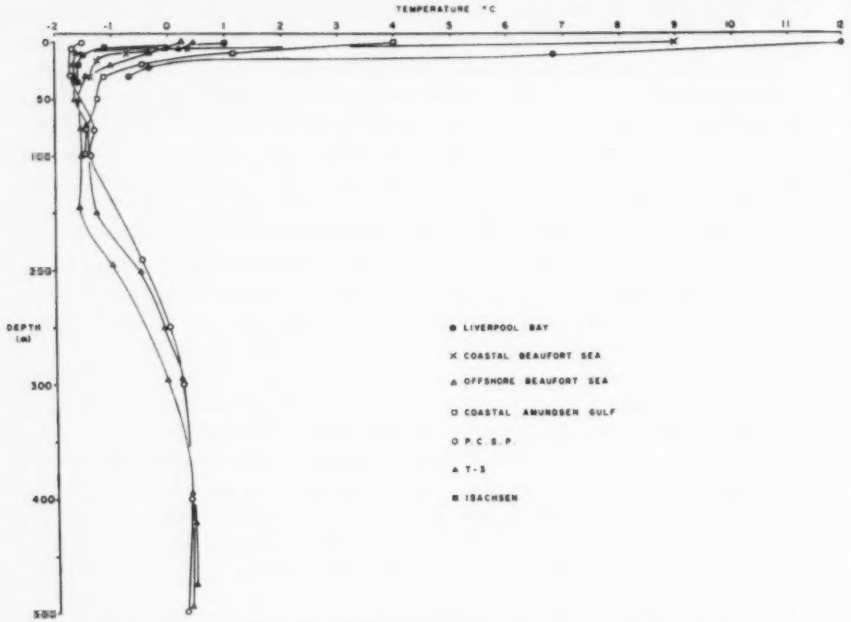


FIG. 2. Temperature diagrams from selected stations in the various collecting areas. Offshore Beaufort Sea curve from Bailey (1957), T-3 and P.C.S.P. curves from Collin (1959, 1961).

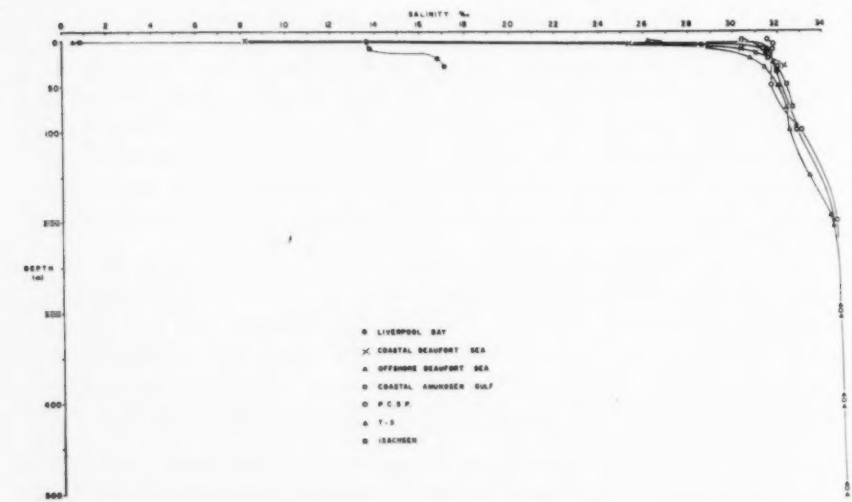


FIG. 3. Salinity diagrams from selected stations in the various collecting areas. Offshore Beaufort Sea curve from Bailey (1957), T-3 and P.C.S.P. curves from Collin (1959, 1961).

The Arctic Ocean is divided into three major horizontal water masses largely on the basis of temperatures: Arctic surface water, Atlantic water, and bottom water (Coachman, 1963). The cold Arctic surface water is described as originating in the Arctic Ocean. Its lowest layer, in the Canadian Basin between about 150 m and the Atlantic water, has properties intermediate to those of the cold Arctic water above and the warmer Atlantic water below. The Atlantic water is described as originating in the Atlantic Ocean. The Atlantic water enters the Arctic basin between Greenland and Spitzbergen, showing its identity most strongly north of Spitzbergen, and least positively off the north Canadian islands and in the Beaufort Sea. Arctic surface water moves out of the Arctic Ocean southward and eastward through the channels separating the Canadian arctic islands and between Canada and Greenland, into Baffin Bay and Davis Strait. There would appear to be a small and thwarted intrusion of Atlantic water from the Arctic Ocean into the relatively deep western end of Parry Channel as well as into portions of other deep channels continuous with the Arctic Ocean such as Amundsen Gulf, Prince Gustaf Adolph Sea, and Peary Channel (U.S. Navy Hydrographic Office, 1958). Because of relatively shallow depth in Barrow Strait however (about 150 m), the circulation from the west through the archipelago to Baffin Bay and Davis Strait appears to be restricted to water of the Arctic surface layer (Collin, 1963). Similarly a limiting depth of about 200 m in Kane Basin presumably restricts under normal conditions the southward flow of Arctic Ocean water between Canada and north Greenland to Arctic surface water.

A fourth water mass is reported from the Arctic Ocean over the Canadian Basin between depths of about 50 and 100 m, and is labelled Pacific water (Coachman and Barnes, 1961). This water, said to enter through Bering Strait, appears to show its strongest characteristics in the Chukchi Sea just north of Bering Strait, its weakest positive characteristics off the northern Canadian islands and in the southeast Beaufort Sea.

ZOOPLANKTON

Present Collections

There were at least 50 species of zooplankton found in the present collections, including 21 species taken on T-3, 24 species in the passages among the northern islands, 28 species in the Beaufort Sea and Amundsen Gulf collections of *Cancolim II*, and 37 species in the generally shallow, coastal collections of the *Salvelinus*. Table I shows horizontal occurrence of all the species recorded here.

The zooplankton may be divided into three groups on the basis of horizontal distribution. The first group comprises species of wide occurrence, having been taken over most of the region shown in Fig. 1. They comprise the major element of the offshore collections (in the present instance the *Cancolim* and T-3 material) and extend as well into the south Beaufort, Amundsen Gulf, and northern shelf regions. Included are the two major pelagic med-

TABLE I. Horizontal occurrence of zooplankton species found in the present collections.

	South Beaufort Sea	Amundsen Gulf	East Beaufort Sea	M'Clure Strait	P. C. S. P.	T-3
Medusae and Siphonophora						
Sarsia princeps (Haeckel)	+	•	•	•	•	•
Euphysa flammea (Linko)	+	•	•	•	•	•
Halitholus cirratus Hartlaub	+	•	•	•	•	•
Eumedusa birulai (Linko)	+	•	•	•	•	•
Ptychogena lactea Agassiz	+	•	•	•	•	•
Obelia sp.	+	•	•	•	•	•
Aglantha digitale (O. F. Müller)	+	+	+	+	•	+
Aeginopsis laurenti Brandt	+	+	•	+	+	+
Dimophyes arctica (Chun)	•	+	•	+	•	•
Ctenophora						
Mertensia ovum (Fabricius)	+	+	•	•	•	•
Beroe cucumis Fabricius	•	+	•	•	•	•
Rotifera						
Unidentified	•	•	•	•	•	+
Polychaeta						
Larvae	+	•	•	•	+	+
Pelecypoda						
Larvae	+	•	•	•	•	•
Pteropoda						
Limacina helicina (Phipps)	+	+	+	+	•	+
Clione limacina (Phipps)	+	+	+	•	•	+
Cladocera						
Podon sp.	+	•	•	•	•	•
Ostracoda						
Conchoecia maxima Brady & Norman	+	•	•	+	•	+
Copepoda						
Nauplii	+	+	+	+	+	+
Calanus hyperboreus Krøyer	+	+	+	+	+	+
Calanus glacialis Jaschnov	+	+	+	+	+	+
Pseudocalanus minutus (Krøyer)	+	+	+	+	+	+
Microcalanus pygmaeus G. O. Sars	+	+	+	+	+	+
Spinocalanus magnus Wolfenden	•	•	•	•	•	+

(*Continued*)

TABLE 1. Horizontal occurrence of zooplankton species found in the present collections.

(*Concluded*)

	South Beaufort Sea	Amundsen Gulf	East Beaufort Sea	M'Clure Strait	P. C. S. P.	T-3
Gaidius brevispinus (G. O. Sars)	•	•	•	•	•	+
Gaidius tenuispinus (G. O. Sars)	+	+	•	+	•	+
Pareuchaeta glacialis (Hansen)	+	+	+	+	+	+
Eurytemora herdmani Thompson & Scott	+	+	•	•	•	•
Metridia longa (Lubbock)	+	+	+	+	+	+
Limnocalanus grimaldi (de Guerne)	+	•	•	•	•	•
Heterorhabdus norvegicus (Boeck)	+	•	•	•	•	•
Acartia clausi Giesbrecht	+	•	•	•	•	•
Acartia longiremus (Lilljeborg)	+	•	•	•	•	•
Oithona similis Claus	+	+	+	+	+	+
Oncaea borealis G. O. Sars	+	•	+	+	+	+
Cirripedia						
Nauplii	+	•	•	•	•	•
Cypris larvae	+	•	•	•	•	+
Mysidacea						
Mysis sp.	+	•	•	•	+	•
Amphipoda						
Pseudalibrotus glacialis G. O. Sars	+	•	•	•	•	•
Pseudalibrotus nanseni G. O. Sars	•	•	•	+	+	•
Gammarus wilkitzki Birula	•	+	•	•	•	•
Gammaracanthus loricatus (Sabine)	•	•	•	•	+	•
Hyperia medusarum (Müller)	+	•	•	•	•	•
Hyperoche medusarum (Krøyer)	+	•	•	•	•	•
Parathemisto abyssorum Boeck	+	+	+	+	•	•
Parathemisto libellula (Mandt)	+	+	•	•	+	•
Euphausiacea						
Thysanoessa raschi (M. Sars)	+	•	•	•	•	•
Decapoda						
Larvae	+	•	•	•	•	•
Chaetognatha						
Sagitta elegans Verrill	+	+	+	•	+	•
Eukrohnia hamata (Mobius)	•	•	•	+	+	+
Larvacea						
Oikopleura vanhoeffeni Lohmann	+	+	+	+	+	+
Fritillaria borealis Lohmann	+	+	•	•	+	+

usae, *Aglantha digitale* and *Aeginopsis laurenti*, the pteropods *Limacina helicina* and *Clione limacina*, the copepods *Calanus hyperboreus*, *C. glacialis*, *Pseudocalanus minutus*, *Microcalanus pygmaeus*, *Pareuchaeta glacialis*, *Metridia longa*, *Oithona similis*, and *Oncaea borealis*, the chaetognath *Sagitta elegans*, and the larvaceans *Oikopleura vanhoeffeni* and *Fritillaria borealis*. The occurrence of this group is illustrated by the copepods *C. hyperboreus* and *M. pygmaeus*, shown in Fig. 4.

The second group comprises species restricted almost entirely to offshore locations. They are few and include the ostracod *Conchoecia maxima*, the

FIG. 4. Horizontal occurrence of six copepod species, showing records from *Burton Island* and Canadian Arctic Expedition stations along with the present collections.

copepods *Spinocalanus magnus*, *Gaidius brevispinus*, *G. tenuispinus*, and *Heterorhabdus norvegicus*, and the chaetognath *Eukrohnia hamata*. The occurrence of this group is indicated in Fig. 4 by *S. magnus* and *G. tenuispinus*.

The third group includes the primarily coastal species, restricted in the present region to the near-shore and shallow waters of the southern Beaufort Sea and southern Amundsen Gulf. Included are the meroplanktonic medusae *Sarsia princeps*, *Euphysa flammea*, *Halitholus cirratus*, *Eumedusa birulai*, *Ptychogena lactea*, and *Obelia* sp., the copepods *Eurytemora herdmani*, *Limnocalanus grimaldi*, *Acartia clausi*, and *A. longiremus*, and the amphipod *Hyperoche medusarum*. This group is represented in Fig. 4 by *E. herdmani* and *L. grimaldi*.

There is some correlation between horizontal and vertical occurrence of the species comprising each of the three groups shown above. All those of the first group (wide offshore and inshore occurrence) were found near the surface as well as deeper. *Calanus hyperboreus* and *M. pygmaeus*, for example, were taken at various depths from immediately beneath the surface to at least 100 m and probably as deep as the present collections reached. Those of the second group (offshore occurrence almost exclusively) were taken only at considerable depth and appear to be almost entirely absent from near the surface. *Gaidius tenuispinus*, although it occurred rarely as shallow as about 20 m, reached by far its greatest numbers below about 200 m. *Spinocalanus magnus* was taken only in vertical hauls which reached to between 200 and 500 m depth. Members of the third group were exclusively near-surface forms and nearly all were taken at stations of 20 m depth or less, the majority within the upper 5 or 10 m. *Eurytemora herdmani* and *L. grimaldi* were found for the most part within the upper metre.

The species fall into the same groups when considered from the point of view of their temperature and salinity ranges. Figure 5 shows approximate ranges of temperature and salinity for selected species in the present collections. The first 17 species listed show generally fairly wide temperature ranges, from less than −1° to about 5-10°C. These are all cold-water species which can tolerate, at least temporarily, fairly considerable temperature rise, of the sort which occurs during summer warming of the surface waters in open areas of the Arctic Ocean and adjacent northern seas. Salinity ranges of the same species are relatively wide. All were taken at 32‰ and higher salinity, and all evidently can tolerate at least temporary salinity reductions to the order of 20‰ and even less.

The six species of the second group in Fig. 5 were found in the present material only in relatively cold water (below about 1°C). They were found too only at high salinity, generally greater than 32‰.

Those of the third group in Fig. 5 are characteristic of relatively high temperatures, from between about 1 and 4°C to a maximum of about 12°C. These species were totally absent from the cold water inhabited by the first two groups. Salinities were all relatively low, all but one (*H. cirratus*, which

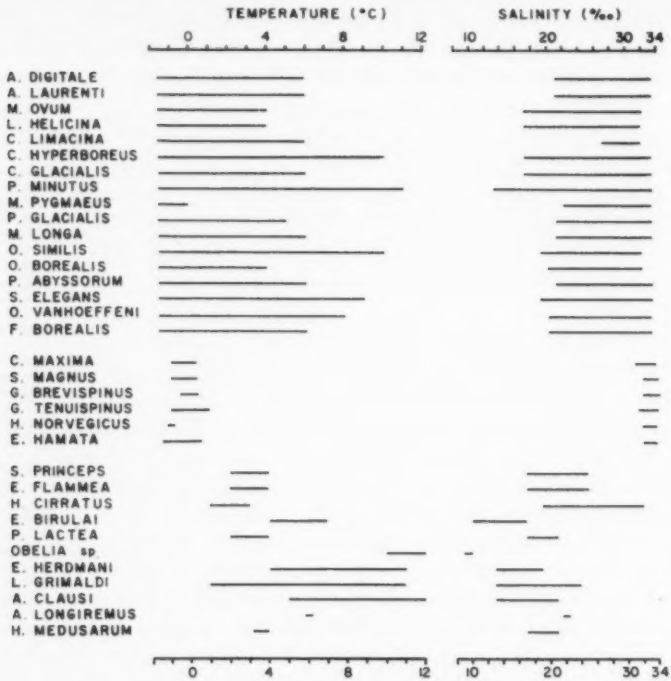


FIG. 5. Approximate ranges of temperature and salinity of selected zooplankton species in the present collections.

appears to have a limited tolerance of higher salinity) having been taken between a maximum salinity of 25‰ and a minimum of 8‰.

Real distinction between the three groups of zooplankters appears to be established on the grounds of horizontal and vertical distribution and temperature and salinity tolerance within the present region. They can also be shown to have validity with respect to wider geographical occurrence, throughout the Arctic Ocean and adjacent seas.

CENTRAL ARCTIC OCEAN AND WESTERN AFFINITIES

Zooplankton records, especially from the *Sedov*, NP 2, and Alpha reports, provide data on the vertical distribution of the various species in the waters of the Arctic Ocean. From all available reports there are about 113 zooplankton species known to inhabit the central Arctic Ocean (excluding the peripheral seas). While data on vertical distribution are few, they are nevertheless adequate to permit identification of the majority of species with one or more of the major horizontal water masses of the Arctic Ocean, that is with the Arctic surface, Atlantic, and bottom water.

Brodsky (1956) pointed out that while the greatest density of zooplankton occupies the cold Arctic surface layer, the greatest number of species inhabits the warmer Atlantic layer of the Arctic Ocean. From the data on vertical occurrence given by Brodsky and Nitikin (1955), Brodsky (1957), and Johnson (1963a), it is clear that about 30 copepod species have been found in the upper 300 m, nearly 50 species have been taken between 300 and 1000 m and about 20 have been found below 1000 m.

In the upper 50 m of the central Arctic Ocean, eight copepod species account for more than 99%, and between 50 and 300 m for more than 95% of the total number of copepod individuals found. They are *Calanus hyperboreus*, *C. glacialis*, *Pseudocalanus minutus* (s.l.), *Microcalanus pygmaeus*, *Pareuchaeta glacialis*, *Metridia longa*, *Oithona similis*, and *Oncaea borealis*. They are the predominant species of the Arctic surface water, and they are most abundant there. Most are found as well in the deeper Atlantic water, but only in considerably smaller numbers than nearer the surface.

A few other species, never found in large numbers, occur predominantly or exclusively in the upper 300 m. Among them are several clearly Pacific species, including *Calanus plumchrus*, *C. cristatus*, *Eucalanus bungii bungii*, and *Metridia pacifica*, found only over the Canadian Basin in the Arctic Ocean.

The remaining central Arctic Ocean species include several which inhabit in very small numbers the lower layer of the Arctic surface water as well as the deeper Atlantic water. *Spinocalanus magnus* has been found rarely as near the surface as the upper 25 m; it is characteristically a deeper species however, found most commonly below 200–300 m. *Gaidius tenuispinus* has been taken occasionally in the upper 50 m, *G. brevispinus* and *Heterorhabdus norvegicus* rarely in the upper 100 m. These three species, however, appear to be more numerous below 100–200 m and in the deeper Atlantic water. *Aetidiopsis rostrata* is almost entirely restricted to depths greater than 200–300 m. A number of other species show similarly sparse occurrence in the lower levels of the Arctic surface water and apparently greater numbers in the Atlantic layer. Others are limited entirely to the Atlantic layer or are found there and in the bottom water as well, and a few are evidently bottom water inhabitants only.

Several copepod species have been reported almost exclusively (north of the Atlantic and the Pacific) from near-surface waters of the marginal seas of the Arctic Ocean. These include *Derjuginia tolli*, *Eurytemora herdmani*, *E. transversalis*, *E. pacifica*, *Limnocalanus grimaldi*, *Epilabidocera amphitrite*, *Acartia clausi*, *A. longiremus*, *A. tumida*, and *Tortanus discaudatus*.

On the basis of vertical distribution over the whole of the central Arctic Ocean and in the adjacent shallow seas three groups of zooplankters may be shown to have significance here: (1) species found in their greatest numbers in the Arctic surface layer; (2) species found primarily in the Atlantic layer as well as in the deep (transitional) level of the Arctic surface water; and (3) species found mainly near the surface in coastal waters. The composition of these three groups may be seen to coincide with the groups defined above on the basis of horizontal and vertical occurrence and temperature and salinity

ranges within the present collections. The widely-occurring, surface-inhabiting group (of the present collections) showing broad temperature and salinity ranges includes all of the predominantly surface water copepod species of the central Arctic Ocean. The primarily offshore, relatively deep-water group of relatively low temperature and high salinity includes only four species of copepods, all of them being species characteristic of the Atlantic and deep Arctic surface level of the central Arctic Ocean. The near-shore, near-surface group of relatively high temperature and low salinity includes four copepods, all established neritic species of adjacent shallow seas.

Johnson (1956, 1963a) has concluded that the best plankton indicators of Pacific water north of Bering Strait are certain "expatriate" species from the Pacific which show no sign of reproduction in the area of expatriation. Several species are listed. Most do not appear to range north of about 75° or east of Point Barrow, Alaska. Two exceptions are *Calanus cristatus*, found off Alaska almost as far to the east as the Alaska–Yukon boundary (about 141°W), and *Eucalanus bungii bungii*, found east to about 144°W in the same area. These species were interpreted by Johnson as indicating the penetration of Pacific water as far east as their points of occurrence.

Somewhat more difficult to interpret is the distribution of certain neritic species east of Point Barrow. Several of these are species of both the Pacific

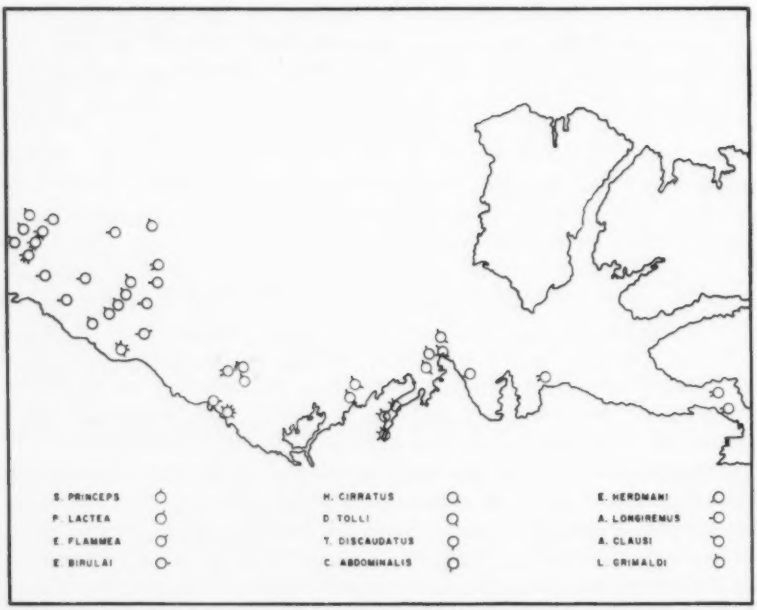


FIG. 6. Records of neritic species of copepods and medusae between the west Beaufort Sea and Dolphin and Union Strait. Records from Bigelow (1920), Willey (1920), Jaschnov (1946), and Johnson (1956) as well as from present collections.

and the Atlantic. A few range from eastern North America eastward around the fringes of the Arctic Ocean to western arctic North America, but not, as far as is yet known, across the north of North America. Included in this group are *S. princeps*, *E. flammea*, *H. cirratus*, *P. lactea*, and *A. longiremus*. Others, such as *E. herdmani*, *A. clausi*, and *H. medusarum*, appear to be restricted to the Chukchi–Beaufort region north of the Pacific and to the region from eastern North America to the Barents Sea north of the Atlantic. *Eumedusa birulai*, not known from the Pacific or Bering Sea, is known from the Kara Sea eastward to the locations reported here. *Limnocalanus grimaldi*, also evidently absent from the Pacific, is also reported from the Kara Sea eastward to the locations given here, as well as from East Greenland, the Baltic, and the Caspian Sea.

Many of the species of the neritic group, including several not listed above, show continuous ranges eastward from Bering Strait to Point Barrow and to various locations between Point Barrow and Dolphin and Union Strait (Fig. 6). Relative abundance of these species in the Chukchi Sea and their gradual numerical reduction towards the east, in the south Beaufort Sea and Amundsen Gulf, along with their apparent absence from the waters of the central Arctic Ocean and the central Canadian arctic, suggests dispersal eastward from the Chukchi Sea as far at least as the records shown here. Further collecting in low-salinity waters between Dolphin and Union Strait and the eastern Canadian arctic is desirable however to confirm the eastern limits indicated here, especially of *Eurytemora herdmani* and *Acartia longiremus*.

Eastern Arctic Affinities

To consider briefly the fauna of the present region with relation to that of waters of the eastern arctic, Table II is given to show records of copepods from Foxe Basin, Ungava Bay, and northwest Baffin Bay along with the present region. Data from the eastern regions are taken from Jespersen (1934), Fontaine (1955), and Grainger (1959, 1962). Several species listed for the eastern regions and not taken in the present collections are known from the Arctic Ocean and are included in Table II as additional central Arctic Ocean records.

The first eight species listed in Table II are the dominant copepods of the surface layer of the Arctic Ocean. Seven of these are reported from Foxe Basin and the upper 50 m of Ungava Bay and all eight are known from the upper 50 m of northwest Baffin Bay. In the three eastern regions as in the Arctic Ocean they are the dominant species of the upper layers. Eight other species only are known in the upper layers of the eastern regions considered here, all of them having clear Atlantic affinities. Included are *Calanus finmarchicus*, *Acartia longiremus*, *Gaidius tenuispinus*, *Pareuchaeta norvegica*, *Eurytemora americana*, *Acartia bifilosa*, *Cyclopina gracilis*, and *C. schneideri*. The remaining species in Table II (excluding the neritic species of the western arctic) are restricted to deep waters of the eastern regions. They are North

TABLE II. Copepods recorded in the present collections and from Foxe Basin, Ungava Bay, and northwest Baffin Bay.

	Present collections and additional central Arctic Ocean records					Foxe Basin	Ungava Bay		Northwest Baffin Bay	
	Arctic surface			Atlantic	Neritic		Upper 50 m	> 100 m	Upper 50 m	> 300 m
	0–25	25–100	100–300							
1. *Calanus glacialis*	+	+	+	r	–	+	+	+	+	?
2. *Calanus hyperboreus*	+	+	+	r	–	+	+	+	+	+
3. *Pseudocalanus minutus*	+	+	+	–	–	+	+	+	+	+
4. *Microcalanus pygmaeus*	+	+	+	r	–	+	+	–	+	+
5. *Metridia longa*	+	+	+	r	–	+	+	+	+	+
6. *Oithona similis*	+	+	+	r	–	+	+	–	+	+
7. *Oncaea borealis*	+	+	+	–	–	+	+	–	+	–
8. *Pareuchaeta glacialis*	+	+	+	r	–	–	–	+	+	+
9. *Calanus finmarchicus*	–	r	r	+	–	r	+	+	r	?
10. *Gaidius tenuispinus*	–	r	+	+	–	r	–	+	–	+
11. *Pareuchaeta norvegica*	–	–	–	+	–	–	r	+	–	+
12. *Spinocalanus magnus*	r[a]	r	r	+	–	–	–	–	–	+
13. *Gaidius brevispinus*	–	–	+	+	–	–	–	–	–	+
14. *Heterorhabdus norvegicus*	–	r	+	+	–	–	–	+	–	+
15. *Aetidiopsis rostrata*	–	–	r	+	–	–	–	+	–	+
16. *Spinocalanus brevicaudatus*	–	–	r	+	–	–	–	–	–	+
17. *Pseudaetideus armatus*	–	r	r	+	–	–	–	–	–	+
18. *Chiridius obtusifrons*	–	–	+	+	–	–	–	–	–	+

19. *Scaphocalanus magnus*	–	r	+	+	–	–	–	–	–	+
20. *Haloptilus acutifrons*	–	–	r	+	–	–	–	–	–	+
21. *Xanthocalanus borealis*	–	–	–	+	–	–	–	–	–	+
22. *Undinella oblonga*	–	–	–	+	–	–	–	–	–	+
23. *Augaptilus glacialis*	–	–	–	+	–	–	–	–	–	+
24. *Gaetanus miles*	–	–	–	–	–	–	–	–	–	+
25. *Pareuchaeta wilsoni*	–	–	–	–	–	–	–	–	–	+
26. *Pareuchaeta farrani*	–	–	–	–	–	–	–	–	–	+
27. *Pareuchaeta scotti*	–	–	–	–	–	–	–	–	–	+
28. *Lucicutia curta*	–	–	–	–	–	–	–	–	–	+
29. *Heterostylites major*	–	–	–	–	–	–	–	–	–	+
30. *Pachyptilus eurygnathus*	–	–	–	–	–	–	–	–	–	+
31. *Acartia longiremus*	–	–	–	–	+	+	+	–	+	–
32. *Eurytemora herdmani*	–	–	–	–	+	–	–	–	–	–
33. *Limnocalanus grimaldi*	–	–	–	–	+	–	–	–	–	–
34. *Acartia clausi*	–	–	–	–	+	–	–	–	–	–
35. *Cyclopina schneiderei*	–	–	–	–	–	–	+	–	–	–
36. *Pleuromamma robusta*	–	–	–	–	–	–	–	+	–	–
37. *Eurytemora americana*	–	–	–	–	–	–	+	–	–	–
38. *Acartia bifilosa*	–	–	–	–	–	–	+	–	–	–
39. *Cyclopina gracilis*	–	–	–	–	–	–	+	–	–	–

[a]r signifies rare, relative to numbers indicated by + .

Atlantic species, most of which have been found as well in the Atlantic layer of the Arctic Ocean, and seven of which have not yet been reported from the central Arctic Ocean.

Arctic Ocean and the Canadian Arctic

When we consider the zooplankton composition of the Arctic Ocean, the Beaufort Sea, the western Canadian arctic, and the eastern arctic, it is apparent that there is a remarkable homogeneity within the upper 100–300 m over the entire region. Eight species of copepods, along with two each of medusae, pteropods, and larvaceans and one chaetognath, not listed in Table II, comprise the very great majority of the total number of individuals found in surface waters from the Arctic Ocean to the eastern Canadian arctic and Baffin Bay. These are the principal "arctic" species of the cold waters adjacent to the Arctic Ocean, the indicators of southward movement of Arctic surface water between Canada and Greenland, east of Greenland, and northwest of Europe.

Deeper, in the Arctic Ocean, a much larger group of species comprising nevertheless far fewer individuals inhabits the intermediate Atlantic layer and to a lesser extent the deep level of the Arctic surface layer. Many of the same species are present in the intermediate water of Baffin Bay, and enter the waters of the eastern arctic from Davis Strait. Some of them enter Hudson Strait with the mixed West Greenland and Baffin Island current, and appear in the deeper waters of Ungava Bay, and a few appear to follow a continuation of this circulation through Hudson Strait and into Foxe Basin. Members of this group, however, appear to be very largely excluded from most of the waters of the Canadian archipelago by limiting depths and the prevailing circulation pattern of the Arctic Ocean surface water.

Development of Copepods in the Arctic Ocean

Some data on the development of two of the major Arctic Ocean copepods are available from T-3 and Isachsen. The most abundant copepod at T-3 was *Microcalanus pygmaeus*, which along with *Oncaea borealis* accounted for well over one-half the total number of copepods collected.

In the Isachsen and T-3 material (Fig. 7a, b) stage I was present at least by late June, although it did not achieve maximum numbers until late July. Stage II reached its maximum in late August, and stage III, evidently as a continuation of the preceding developing series, appeared in early September and reached relative abundance by the middle of September. The representatives of stage III found from near the middle of July until near the middle of August, and of stage IV which were abundant from late June until late July, may indicate an earlier developing sequence than the first three stages described above or an overwintering population. The second alternative would appear to be the more likely one.

It is suggested that the main breeding activity takes place at least as early as June and possibly before, that development during the first summer

of at least part of the population reaches only to stage III and perhaps stage IV, and that development is completed not earlier than during the second summer. Part of the population may achieve stage V by late autumn and stage VI during the winter, to give rise to the new generation of the next spring. Part at least appears not to have grown beyond stage IV by the time the next generation is in evidence. These then would appear to develop to breeding condition only at an age of between 1 and 2 years.

From the *Sedov* (Fig. 7c; data from Bogorov, 1946) stage I was present in early June. Stage II achieved maximum numbers in late August, stage

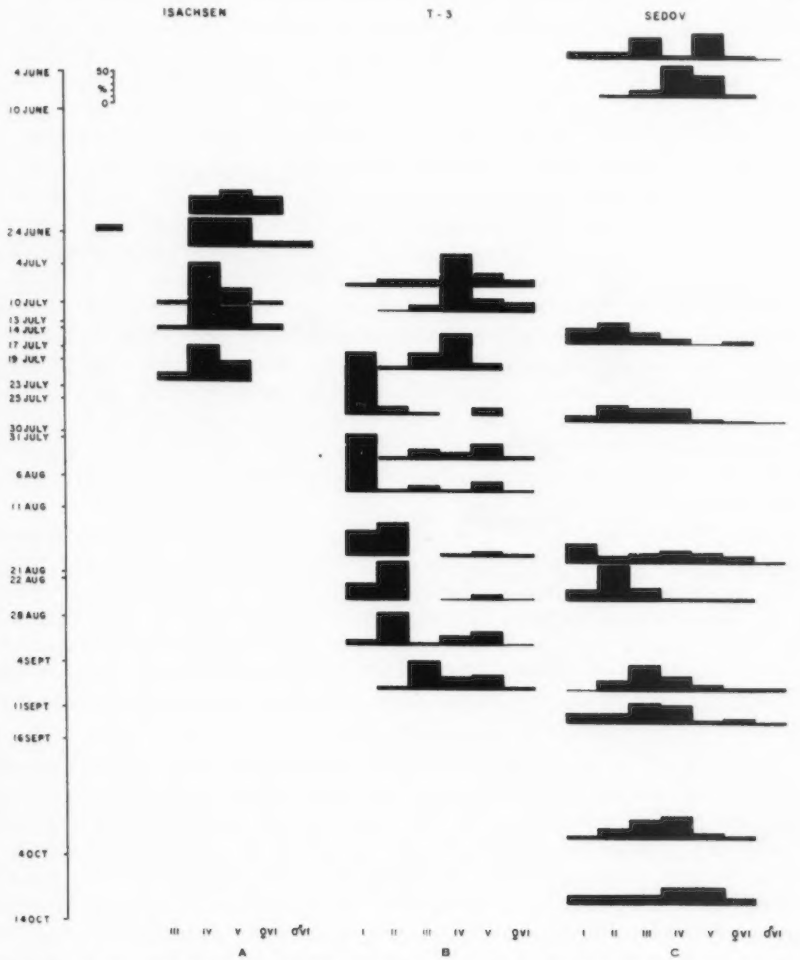


FIG. 7. Copepodite stages of *Microcalanus pygmaeus* in the Isachsen collections (A), the T-3 collections (B), and *Sedov* collections (C).

III in early September, and stages IV and V in early October. There is the suggestion here, as at Isachsen, of overwintering members of stages III–V being present in early June, thus evidence of at least part of the population undergoing a cycle of more than 1 year duration.

Digby (1954) interpreted a 1-year cycle for *M. pygmaeus* of East Greenland. Nearly all nauplii and most copepodites of the first few stages developed in East Greenland before spring phytoplankton growth was under way, a feature evidently characteristic of the species according to Heinrich (1961). If the timing of relative abundance of phytoplankton indicated by Apollonio (MS, 1958) for T-3 in 1957 and by English (1963) for Alpha in 1957 and 1958 applies to T-3 in 1958, then it appears as if at least nauplius production in *M. pygmaeus* may occur in the Arctic Ocean in the almost total absence of phytoplankton, but that at least the major development of the youngest copepodite stages may occur during relative phytoplankton abundance.

Calanus glacialis was the fifth most abundant copepod on T-3, following *M. pygmaeus*, *Oncaea borealis*, *Oithona similis*, and *Calanus hyperboreus*. From the present collections it appears that at T-3 and Isachsen (Fig. 8a, b) the first new members of stage I develop from nauplii in late July and early August. Development to stage II occurs by early September. There is evidence that the majority of individuals may not progress further than stage III during their first summer, that they may winter at least as young as stage III, and continue development only during the second summer. The prevalence of stages III–V during the late June and July nauplius production period indicates overwintering individuals which probably complete their development only during their second summer, and so produce a new generation at the age of about 2 years. At T-3 the species appeared to pass through all the nauplius stages and at least the first two copepodite stages during the period of relatively abundant phytoplankton.

From the *Sedov* (Fig. 8c; data from Bogorov, 1946, given as *C. finmarchicus*) copepodite I development apparently had begun by early June. Stage I was dominant by the end of July, stage II in early September, and stage III by the middle of October. Wintering probably occurred in stages III–VI. This cycle appears to resemble fairly closely the development of the same species in Foxe Basin (Grainger, 1959, as *C. finmarchicus*), from where it was inferred that part of the population went through an annual cycle while part required 2 years to complete development.

Heinrich (1961) set up several groups of copepods on the basis of the relation between times of breeding and development and of phytoplankton (food) abundance. Two of the eight principal Arctic Ocean surface species (*Calanus glacialis* and *Pseudocalanus minutus*) were placed in the group in which breeding occurs simultaneously with phytoplankton abundance. Four of the remaining six species (*Calanus hyperboreus*, *Microcalanus pygmaeus*, *Metridia longa*, and *Oithona similis*) were included among those in which breeding may occur in the absence of phytoplankton, or at least under conditions of extreme phytoplankton scarcity. Of the two remaining species, *Pareuchaeta glacialis*

may almost certainly be included in the second group (*P. norvegica* and *P. japonica* are) and *Oncaea borealis* may be placed with some doubt in the second group on the basis of Digby's (1954) data from Greenland.

Pseudocalanus minutus is rare in the present collections and its breeding and development in the Arctic Ocean have not been described. *Calanus glacialis* (above) appears to show in the Arctic Ocean its customary dependence

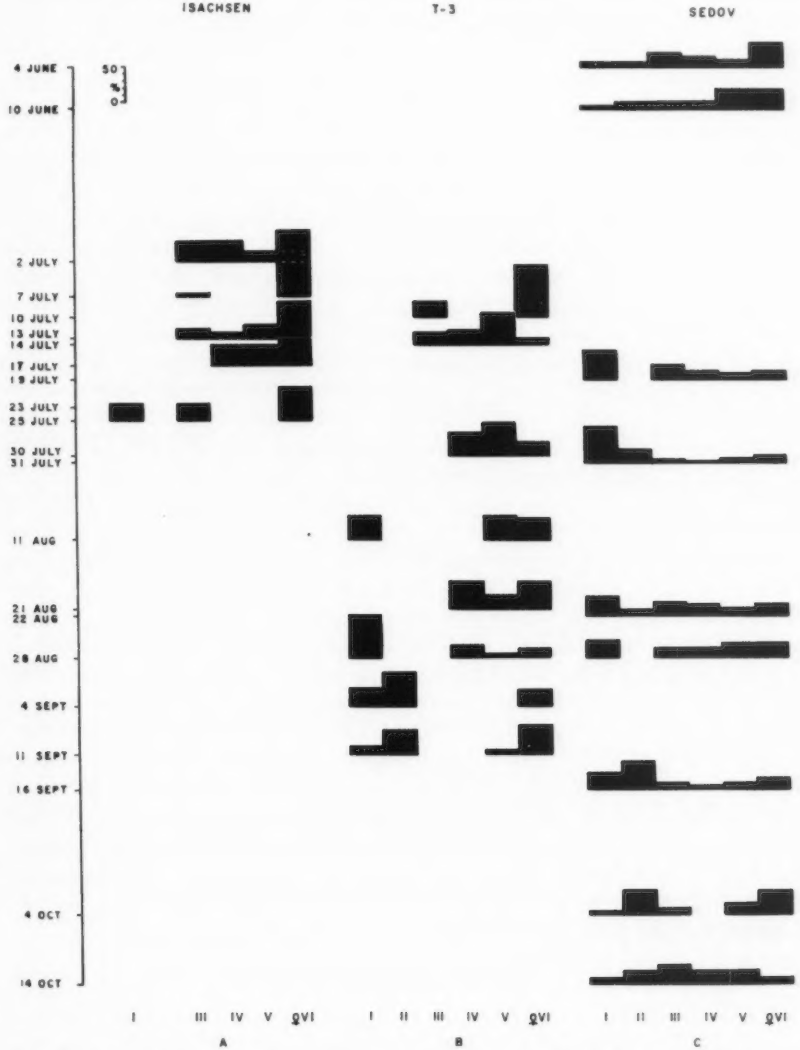


FIG. 8. Copepodite stages of *Calanusglacialis* at Isachsen (A), T-3 (B), and from the *Sedov* (C).

upon phytoplankton for nauplius and early copepodite development. Brodsky and Nitikin (1955) found stage I copepodites only in July and August and more than one-half their stage II individuals in the same months.

Microcalanus pygmaeus in the present material appeared to begin its development before the onset of summer phytoplankton growth. *Calanus hyperboreus* was found in stage I by Brodsky and Nitikin (1955) in every month of the year, and in its greatest numbers in June. Data on *M. longa* given by Brodsky and Nitikin suggest a long period of breeding, occurring at least in part during the winter. There is no information available on breeding and development of *O. similis* in the Arctic Ocean; it appears eleswhere however to breed over much of the year, although evidently it develops its largest populations during the period of phytoplankton abundance. *P. glacialis* is a predatory species. Other members of the same genus are described as breeding throughout the year. In the Arctic Ocean, Brodsky and Nitikin (1955) found stage I copepodites in nearly every month of the year and the greatest numbers in June. Johnson (1963a) also showed the greatest numbers of stages I and II in June and found as well females carrying egg sacs and spermatophores in June and September, a male holding a spermatophore in February, and nauplii especially abundant in February.

Brodsky and Nitikin (1955) found only very rarely copepodites younger than stage IV of species other than those listed above. *Scaphocalanus magnus* (stages II–III) occurred on one occasion between 50 and 100 m, on two occasions between 100 and 300 m. *Gaidius tenuispinus* (stages I–III), *Heterorhabdus norvegicus* (stage II) and *Temorites brevis* (stage III) were found on a few occasions between 100 and 300 m. *Lucicutia polaris* (stages I and III) was taken twice between 300 and 1000 m. *Spinocalanus magnus* (stages I–III), *S. longicornis* (stage III), *S. elongatus* (stage III), *Aetidiopsis rostrata* (stages I and III), and *Chiridiella reducta* (stage II) were found only rarely deeper than 900 m.

The major Arctic surface copepod species appear to be the principal and possibly the only species which breed in the upper waters of the Arctic Ocean. Most of them evidently breed over a fairly long period of the year, independent of phytoplankton quantity, while in only one or two species does breeding apparently coincide with phytoplankton abundance. Some of the deeper Atlantic species may breed to a limited extent in the subsurface waters of the Arctic Ocean. They appear however to be very largely bound to the Atlantic water mass and to be unable to establish breeding populations in the uppermost layers of the Arctic Ocean surface water. It remains to be shown what factors bind these species to the Atlantic water and prevent their successful occupation of the surface water layer.

ACKNOWLEDGMENTS

I wish to thank Dr A. E. Collin for plankton collections from Ice Island T-3 and stations of the Polar Continental Shelf Project, Dr A. H. Lawrie for material taken on the M.V. *Cancolim II*, and Mr J. J. Butters for collections

from the CCGS *John A. MacDonald*. For the 1960 Isachsen collecting opportunity I am indebted to Dr E. F. Roots, Co-ordinator, and many others who took part in the field activities of the Polar Continental Shelf Project of that year.

REFERENCES

APOLLONIO, S. MS, 1958. Hydrological measurements on T-3, 1957–58. Woods Hole Oceanogr. Inst., 7 pp.

BAILEY, W. B. 1957. Oceanographic features of the Canadian archipelago. *J. Fish. Res. Bd. Canada*, **14**(5): 731–769.

BARNARD, J. L. 1959. Epipelagic and under-ice amphipods of the central arctic basin. Scientific studies at Fletcher's Ice Island, T-3, (1952–1955), vol. 1. *Geophys. Res. Papers*, No. 63, pp. 115–152. Geophys. Res. Dir., United States Air Force, Bedford, Mass.

BIGELOW, H. B. 1920. Medusae and Ctenophora. *Rep. Canadian Arctic Exped. 1913–18*, **8**(H): 22 pp.

BOGOROV, V. G. 1946. Zooplankton collected by the "Sedov" expedition 1937–1939. *In* Dreĭfuiushchaĭa ekspeditsiĭa Glavsevmorputi na ledokol'nom parokhode "G. Sedov" 1937–1940 gg., Trudy, **3**: 336-370.

BRODSKY, K. A. 1956. Life in the deep waters of the polar basin. *Priroda*, **5**: 41–48. [Translation by Amer. Meteorol. Soc.]

1957. The copepod fauna (Calanoida) and zoogeographic divisions of the North Pacific Ocean and adjacent waters. Akad. Nauk CCCP, 225 pp.

BRODSKY, K. A., AND M. N. NITIKIN. 1955. Hydrobiological work. Materialy nabliudeniĭ nauchno-issledovatel'skoĭ dreĭfuiushcheĭ stantsii 1950/51 goda, [ed.] M. M. Somov, Izd. 'Morskoĭ transport', **1**: 401–410. [Translation by Amer. Meteorol. Soc.]

COACHMAN, L. K. 1963. Water masses of the arctic. Proc. Arctic Basin Symposium October 1962. Arctic Institute of North America, pp. 143–167.

COACHMAN, L. K., AND C. A. BARNES. 1961. The contribution of Bering Sea water to the Arctic Ocean. *Arctic*, **14**(3): 147–161.

COLLIN, A. E. 1959. Canadian oceanographic activities on IGY drift station "Bravo". *Fish. Res. Bd. Canada, MS Rep. (Oceanogr. and Limnol.)*, No. 40.

1961. Oceanographic activities of the Polar Continental Shelf Project. *J. Fish. Res. Bd. Canada*, **18**(2): 253–258.

1963. The waters of the Canadian arctic archipelago. Proc. Arctic Basin Symposium October 1962. Arctic Institute of North America, pp. 128–136.

DALL, W. H. 1925. Pteropoda. *Rep. Canadian Arctic Exped. 1913–18*, **8**(B): 9–12.

DIGBY, P. S. B. 1954. The biology of the marine planktonic copepods of Scoresby Sound, East Greenland. *J. Animal Ecol.*, **23**(2): 298–338.

ENGLISH, T. S. 1963. Some remarks on Arctic Ocean plankton. Proc. Arctic Basin Symposium October 1962. Arctic Institute of North America, pp. 184–196.

FONTAINE, M. 1955. The planktonic copepods (Calanoida, Cyclopoida, Monstrilloida) of Ungava Bay, with special reference to the biology of *Pseudocalanus minutus* and *Calanus finmarchicus*. *J. Fish. Res. Bd. Canada*, **12**(6): 858–898.

GRAINGER, E. H. 1959. The annual oceanographic cycle at Igloolik in the Canadian arctic. 1. The zooplankton and physical and chemical observations. *J. Fish. Res. Bd. Canada*, **16**(4): 453–501.

1962. Zooplankton of Foxe Basin in the Canadian arctic. *Ibid.*, **19**(3): 377–400.

GRICE, G. D. 1962. Copepods collected by the Nuclear Submarine *Seadragon* on a cruise to and from the North Pole, with remarks on their geographic distribution. *J. Mar. Res.*, **20**(1): 97–109.

HAND, C., AND L. B. KAN. 1961. The medusae of the Chukchi and Beaufort Seas of the Arctic Ocean, including the description of a new species of *Eucodonium* (Hydrozoa: Anthomedusae). *Arctic Inst. North America, Tech. Paper*, **6**: 23 pp.

HARDY, A. C. 1936. The arctic plankton collected by the Nautilus expedition, 1931. Part 1 — General account. *J. Linn. Soc., Zool.*, **39**: 391–403.

HEINRICH, A. K. 1961. Seasonal phenomena in plankton of the World Ocean. 1. Seasonal phenomena in the plankton of high and temperate latitudes. *Tr. Inst. Okeanol., Akad. Nauk SSSR*, **51**: 57–81.

JASCHNOV, V. A. 1946. The distribution of the autochthonous pelagic fauna of the arctic. *Biull. Moskovskogo Obshch. Ispyt. Prirody, Otd. Biologi*, **51**(6): 40–50.

JESPERSEN, P. 1934. Copepoda. The Godthaab Expedition 1928. *Medd. Grønland*, **79**(10): 156 pp.

JOHNSON, M. W. 1953. Studies on plankton of the Bering and Chukchi Seas and adjacent areas. *Proc. 7th Pacific Sci. Congress* (1949), **4**: 480–500.

1956. The plankton of the Beaufort and Chukchi Sea areas of the arctic and its relation to the hydrography. *Arctic Inst. North America, Tech. Paper*, **1**: 32 pp.

1958. Observations on inshore plankton collected during summer 1957 at Point Barrow, Alaska. *J. Mar. Res.*, **17**: 272–281.

1963a. Zooplankton collections from the high Polar Basin with special reference to the Copepoda. *Limnol. Oceanogr.*, **8**(1): 89–102.

1963b. Arctic Ocean plankton. Proc. Arctic Basin Symposium October 1962. Arctic Institute of North America, pp. 173–183.

KNOX, G. A. 1959. Pelagic and benthic polychaetes of the central arctic basin. Scientific studies at Fletcher's Ice Island, T-3, (1952–1955), vol. 1. *Geophys. Res. Papers*, No. 63, pp. 105–114. Geophys. Res. Dir., United States Air Force, Bedford, Mass.

MOHR, J. L. 1959. Marine biological work. *Ibid.*, pp. 83–103.

SARS, G. O. 1900. Crustacea. *The Norwegian North Polar Expedition 1883–96*, **1**(5): 137 pp.

SCHMITT, W. L. 1919. Schizopod crustaceans. *Rep. Canadian Arctic Exped. 1913–18*, **7**(B): 8 pp.

SHOEMAKER, C. R. 1920. Amphipods. *Rep. Canadian Arctic Exped. 1913–18*, **7**(E): 30 pp.

U.S. NAVY HYDROGRAPHIC OFFICE. 1958. Oceanographic atlas of the polar seas. Part II. Arctic. Washington, 139 pp.

WILLEY, A. 1920. Marine Copepoda. *Rep. Canadian Arctic Exped. 1913–18*, **7**(K): 46 pp.

Life History and Ecology of American Plaice (*Hippoglossoides platessoides* F.) in the Magdalen Shallows[1,2]

By P. M. Powles

Fisheries Research Board of Canada
Biological Station, St. Andrews, N. B.

ABSTRACT

Males reach marketable size (32 cm) at age 10, and females at age 8. Sexual maturity is attained at 25 cm (age 6) for males and 41 cm (age 10) for females, and maximum spawning occurs annually from mid April to mid May. Commercial fishing has reduced the number of year-classes in the fishery from about 26 in 1957 to 17 in 1961, but has not affected the rate of growth.

The main summer fishery occurs in the Chaleur Bay, Shippegan Gully, and North Bay regions in depths of 40–100 m. In winter, American plaice were most abundant in depths of 180–460 m (bottom temperature 3–6°C), although a few immatures remained in the cold inshore waters. In spring (April), plaice were taken mostly from 75 to 150 m depths (–1.0 to 5.0°C).

Adult plaice feed mainly on molluscs and echinoderms, and young plaice on polychaetes and small crustacea. Feeding ceases almost completely during January–March. The main food competitor of plaice in the Magdalen Shallows is the Atlantic cod, which has the same general distribution during the summer. Atlantic cod, particularly those over 78 cm long, are also the main predators of small plaice, but mortality due to cod grazing has decreased in recent years because of declining numbers of large cod.

Tagging and meristic studies indicate that Magdalen Shallows plaice are a discrete stock made up of two main groups. The groups are maintained by the tendency of plaice (excluding very old individuals) to return to the same areas each summer. The northern or "Miscou–Magdalen" group includes fish of Chaleur Bay, Shippegan Gully, and Orphan Bank regions. The southern or "Cape Breton" group occurs from George Bay to St. Paul Island.

CONTENTS

	Page
Abstract	565
Introduction	566
Area of Investigation	566
Methods	566
Biology of the Adult Stock	568
Division of Stock	585
Summary	593
Acknowledgments	594
References	594
Appendix 1	596
Appendix 2	597

[1]Received for publication September 25, 1964.
[2]Based on part of a thesis accepted by the Marine Sciences Centre, Faculty of Graduate Studies and Research, McGill University, in partial fulfilment of the requirements for the degree of Doctor of Philosophy.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

INTRODUCTION

THE AMERICAN PLAICE, *Hippoglossoides platessoides* F., is a common subarctic flounder found along the Atlantic coast of North America from Cape Cod to Hamilton Inlet, Labrador. Commercial landings statistics reveal that it is particularly abundant on the Grand Bank, in the Gulf of St. Lawrence, and on the eastern Nova Scotian fishing banks.

The southwestern Gulf of St. Lawrence or "Magdalen Shallows" (International Commission for the Northwest Atlantic Fisheries statistical division 4T) supports an important plaice fishery which, in 1960, produced 25 million lb of marketable fish. An even more profitable cod fishery is sustained in this area, where the distribution of plaice and cod overlaps closely during the summer months.

Development of the Magdalen Shallows plaice fishery started with the introduction of the first offshore otter trawler in 1947. Prior to this, only a few plaice were landed as incidental catches from the hook and line fishery for cod. With the introduction and subsequent expansion of an otter trawler fleet, plaice had risen rapidly to commercial importance by the mid 1950s.

In the present paper the biology of American plaice in the Magdalen Shallows is presented and some ecological observations are included. Details concerning the commercial fishery (Powles, MS, 1964) have been avoided except for brief references where necessary. Comparisons of data on growth and year-classes with similar data of Huntsman (1918) are also included.

AREA OF INVESTIGATION

The southwestern Gulf of St. Lawrence, termed the Magdalen Shallows, was the principal area studied (Fig. 1A). This roughly circular body of water lies west or inside a 500-m trench, the Laurentian Channel. The boundaries and physical characteristics, including the oceanography, have been well described by Lauzier (1957), Hachey (1961), and Steele (1957).

Three water layers are characteristic of the Magdalen Shallows. A deep, stable, "warm"-water layer (3–6°C) underlies an "intermediate" cold-water layer (less than 0°C during the warmer months) which occurs under the thermocline. The surface layer (delimited by the top of the thermocline) is warm in summer and extremely cold in winter when fast or drifting ice covers the area. In late summer therefore, sea floor temperatures in the Magdalen Shallows may fluctuate rapidly, depending on whether the sloping bottom comes in contact with the warm surface or cold intermediate layers.

METHODS

In 1957 the Fisheries Research Board of Canada at St. Andrews, N. B., initiated a series of groundfish research cruises in the Magdalen Shallows. The data collected by various investigators, including the author, during these surveys and special plaice cruises are the main framework of this study.

Three research vessels were used: The *J. J. Cowie* (65 ft), equipped with standard $\frac{3}{4}$ #35 Yankee otter trawl and cover, was used in 1957 and 1958. From 1959 to 1961 the *Harengus* (84 ft) replaced the *J. J. Cowie*, fishing with a #36 Yankee otter trawl and liner. From 1960 to 1962 the *A.T. Cameron*

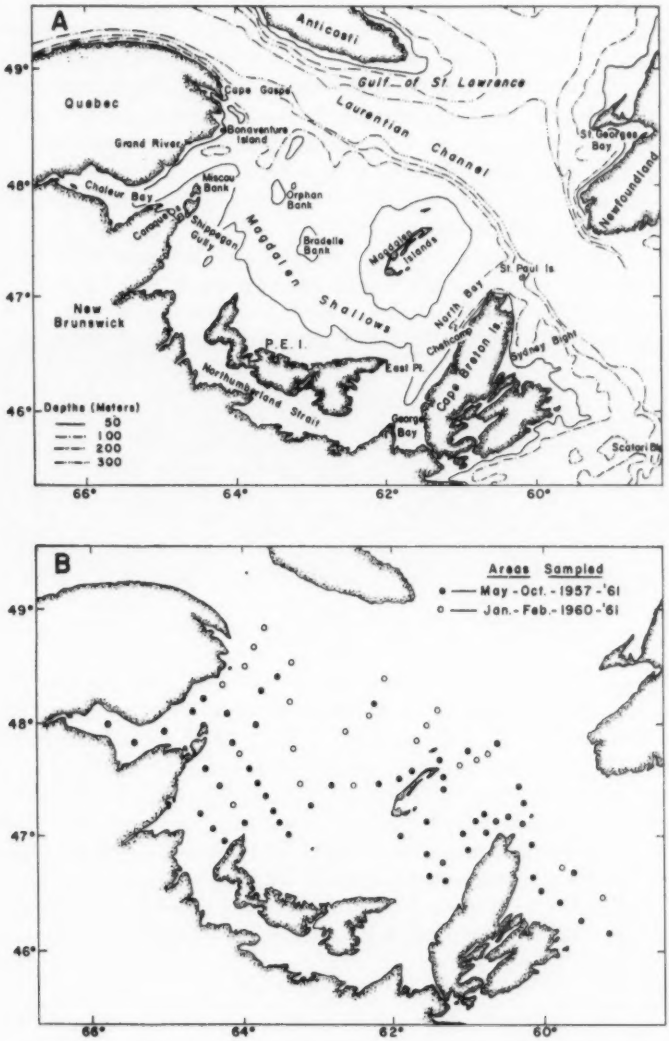


FIG. 1. Map of the western Gulf of St. Lawrence and eastern Nova Scotian area. **A.** Localities referred to in the text. **B.** Locations of the regular sampling stations.

(177 ft), with #41.5 Iceland trawl and small mesh liner, carried out winter operations.

Results of comparative fishing experiments were used to "equalize" catches of the three vessels. The ½-hr *Harengus* tow was chosen as "standard," which necessitated increasing *J. J. Cowie* sets by 1.70 and reducing *A. T. Cameron* tows by 0.57.

During research cruises the numbers, lengths, and sex of plaice caught were recorded. Lengths to the nearest centimetre were measured from the tip of the snout to the longest caudal ray. Maturity stages recorded are outlined in Appendix 1. Both otoliths were removed and stored in a 50% solution of glycerin and water. Food volumes in stomachs were generally estimated in the field by constant reference to standard clay cubes of known volumes. Sea surface and bottom temperatures were recorded and bathythermograph casts were made at all regular stations (Fig. 1B).

For tagging experiments, short tows (15–30 min) were made and any fish caught were held in a tank containing running sea water. Those in good condition were tagged, held in a similar tank for observation, and released. Petersen-type vinyl discs, 18 mm in diameter, were attached by a stainless steel pin through the dorsal musculature as by McCracken (1957). Lengths of tagged fish were measured to the nearest millimetre. Fishermen were advised of the tagging program by posters and radiotelephone conversations.

BIOLOGY OF THE ADULT STOCK

GROWTH

VALIDITY OF THE AGEING TECHNIQUE. Hyaline rings in the otolith were counted using a stereoscopic microscope and blue reflected light (Fig. 2). Several methods were used to show that the rings were true annuli, formed in winter (Powles, MS, 1964). Two of these validation techniques are presented here.

The first method of validation was comparison of the growth of tagged plaice with growth obtained from mean length-at-age data. Growth increments of plaice liberated in 1958 (recaptured a year later) were compared with increments obtained from the mean length-at-age data of surveys in 1958 and 1959. Both types of information were transferred to straight-line relationships as described by Walford (1946) and Manzer and Taylor (1947). A shrinkage factor of 1.2% was added to the lengths of recaptured fish as suggested by Lux (1960) since all were returned dead, whereas survey fish were measured alive. Only females were plotted (Fig. 3) since the number of males recaptured was very low. The tagging data, by least squares fit, gave the following equation:

$$L_{t+1} = 0.92L_t + 4.9.$$

The mean length-at-age data fit the equation

$$L_{t+1} = 0.89L_t + 5.2.$$

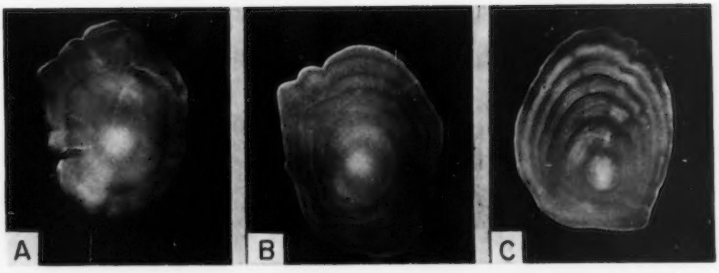


FIG. 2. Otoliths of American plaice from two areas. **A.** Female specimen 22 cm long, age 3 +, Cape Cod region (courtesy F. Lux). **B.** and **C.** Female 25 cm long, 6 +, Magdalen Shallows.

Powles — J. Fish. Res. Bd. Canada

The growth lines obtained from the tagging data and from the mean length-at-age data showed close agreement.

Consistency of strong and weak year-classes over several years was used as evidence for the second method of validation. Ages for this study were also determined from plaice otoliths taken during surveys (Fig. 4). Among Chaleur Bay fish older than 6 years in 1957, the 1950 year-class was dominant, and it continued to be stronger than its neighbouring year-classes through to 1961. The 1953 year-class also appeared prominent, and could be followed from 1957 through 1961. Although there were more large fish in North Bay (Fig. 4) than in either Chaleur Bay or Sydney Bight, the 1950, 1953, and 1954 year-classes were strong in the first two regions. The 1949 and 1951 year-classes were consistently weak in all regions. The consistencies of year-classes obtained from examination of otoliths were also in close agreement between years. The otolith method of determining ages for American plaice is therefore considered reliable.

RATE OF GROWTH. A graphical presentation of $L_{t+1} = L\infty\,(1-k) + kL_t$ (Walford, 1946), with L_{t+1} plotted against L_t, showed that from age 1 onwards the lengths conformed to a linear series. The lines for male and female inter-

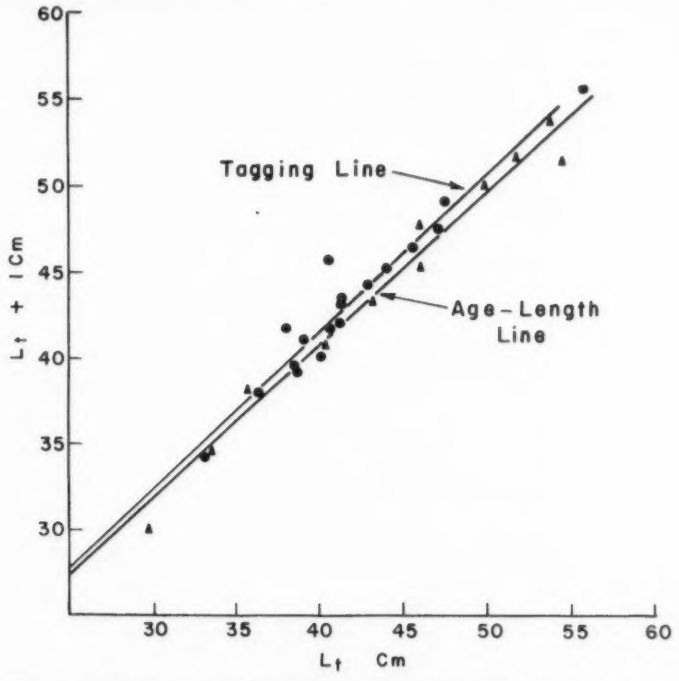


FIG. 3. Straight line growth transformations of American plaice from tagging and age–length data. Total lengths (L_t) are plotted against lengths one year later (L_{t+1}). Triangles indicate mean length-at-age, while circles represent lengths of individual (tagged) fish.

cepted the 45° line at 46 and 71 cm, respectively, representing the asymptotic lengths for American plaice. A von Bertalanffy (1938) curve was then fitted to the data in the manner outlined by Ricker (1958). In the formula

$$L_t = L\infty\left[1-e^{-k(t-t_0)}\right]$$

L_t is the length at any age t, $L\infty$ is the average maximum or asymptotic length of the fish, k is the slope, and t_0 is the time at which the fish would have been zero length if it had always grown in the manner described by the equation.

The equations representing the growth of American plaice in the Magdalen Shallows were found to be:

$$L_t = 45.5\ \left[1-e^{-.15(t-.35)}\right]\ \text{(males)}$$

$$L_t = 70.6\ \left[1-e^{-.09(t-.36)}\right]\ \text{(females)}.$$

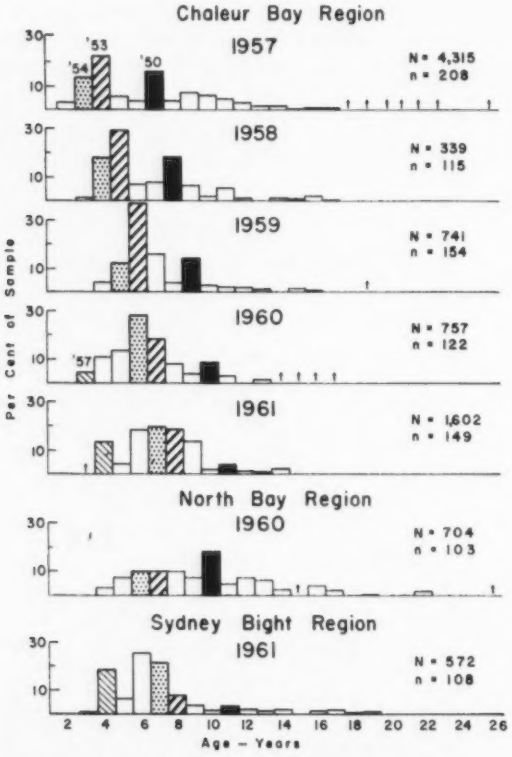


FIG. 4. Age composition of American plaice (females) in the Magdalen Shallows (Chaleur and North Bay) and Sydney Bight areas. Data are from research-vessel surveys, May–July period. N is the total number of fish caught, and n is the number of otoliths read.

Variations in the growth rates between year-classes could not be demonstrated, and therefore the data for fish of the same age were treated together for the years available. Growth rates between various localities within the Magdalen Shallows were similar, although there was some tendency for the growth to be slower in deeper waters (Fig. 5).

Males and females maintained a similar growth rate up to the fourth year, but beyond this age males grew more slowly than females and did not live as long. To reach commercially acceptable size (32 cm long), the males require 10 years, and females 8 years. Because of the combination of slow growth and great body width, smaller plaice are exposed to the otter-trawl fishery long before they are marketable, since they cannot escape through the meshes of trawls currently in use (Powles, MS, 1964).

In other areas the growth rate may differ considerably. Huntsman (1918) indicates that growth is more rapid to the south, and Lux (personal communication) has shown that it is more rapid in waters off Cape Cod (Fig. 6). The otolith shown in Fig. 2A suggests that the growth rate off Cape Cod is almost twice that of plaice in the Magdalen Shallows. Surprisingly, the growth rate off Labrador (Yanulov, 1962) does not appear to differ greatly from that in the Magdalen Shallows (Fig. 6). Bagenal (1955) has already indicated that

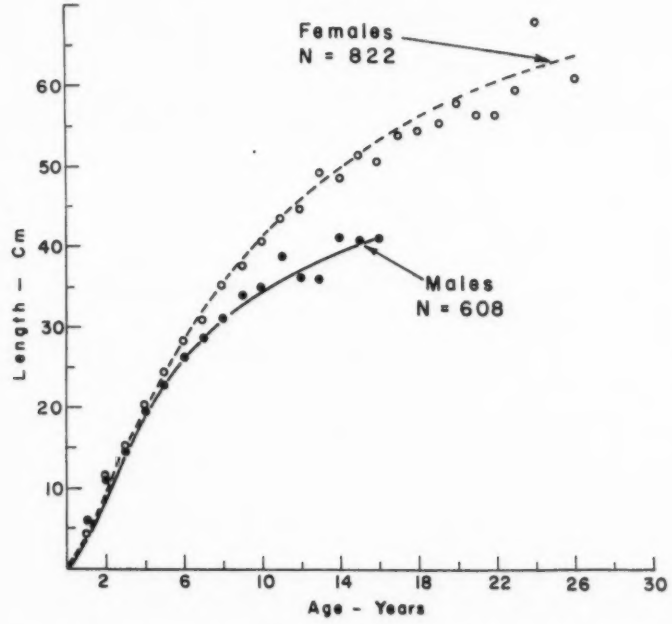


FIG. 5. The increase in length of American plaice with age, represented by the von Bertalanffy growth curve. Data are from research-vessel surveys in the Magdalen Shallows for the period August–October, 1957–61, combined.

the longevity of *Hippoglossoides platessoides* in European waters is less than that for American waters.

CHANGES IN GROWTH AND AGE COMPOSITION. For the period 1917–45 no data are available on American plaice in the Magdalen Shallows. Commercial samples taken by the Fisheries Research Board, including length, sex, and otoliths of plaice, were available from as far back as 1946. These samples were examined and the ages were determined by the author. No appreciable changes in growth rate were apparent from the 1947 and 1960 samples (Fig. 7). Huntsman (1918) used scales to age American plaice in the Magdalen Shallows in 1917. Kohler and Clark (1958) showed that, for haddock, ages determined from scales are comparable with those from otoliths only over the younger age-range. Among older fish, the outer scale annuli become indistinct or fused, but comparable outer annuli tend to be distinct in an otolith. Although similar comparisons have not been made between plaice scales and otoliths, if the same bias holds true, scales from large fish should give lower age readings than otoliths. Scale readings would result in a larger mean length-at-age, and fewer old year-classes.

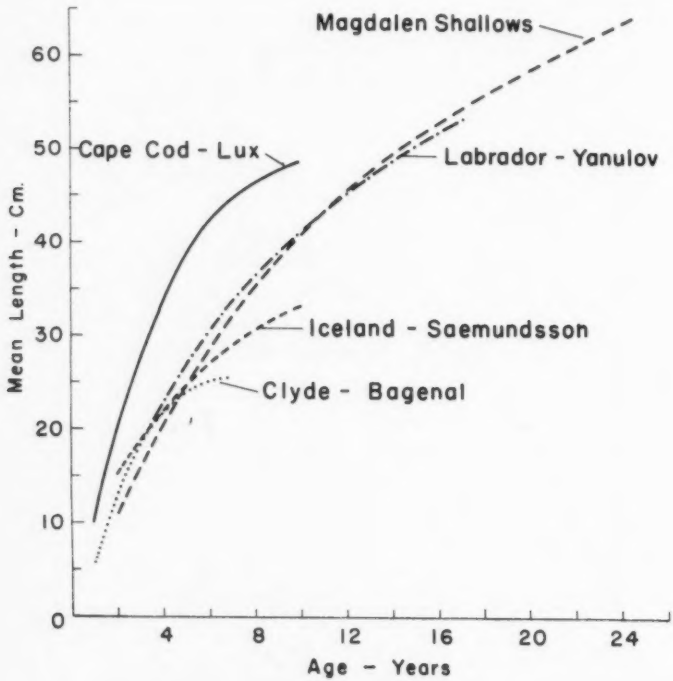


FIG. 6. General age-length relationships for female *Hippoglossoides platessoides* from different areas. Data are from the various authors indicated.

A comparison of the growth rates in 1917 and 1960 from the same locality suggests the 1960 growth rate was more rapid (Fig. 7). Only fish between the ages 4 and 8 years are shown. This age-range was chosen since Huntsman combined the sexes, and little difference in growth rate between the sexes occurs up to age 8 (Fig. 5).

Age compositions of plaice from Huntsman (1918) and from other unpublished records of commercial samples in the Cheticamp area in 1950–56 were compared with those from 1957 and 1960 survey data (Fig. 8). The 1950–56 samples (age determined by the author) have been adjusted to include discards, and are comparable with the others only from age 7 onwards. Admittedly there are inherent dangers involved in such comparisons, particularly since Huntsman aged his fish from scales. However, the data do suggest a decline in the relative abundance of old fish through the years 1917–60.

If this was indeed so, it is consistent with the similar decrease in old fish evident from the 1957–61 surveys in the northern section of the Magdalen Shallows (Fig. 4). All these samples were taken with small-mesh otter trawl, and all otoliths were read by the author.

Size and Age at Maturity

The sizes of Magdalen Shallows plaice in relation to sexual maturity are shown in Fig. 9A. The length at which 50% became mature was calculated by probit analysis (Finney, 1952; Fleming, 1960). Half the females were mature at a length of 41 cm, while half the males were mature at a length of 25 cm. These lengths correspond to ages 10 and 6, for females and males, respectively. Apparently the commercial fishery is mainly dependent on ma-

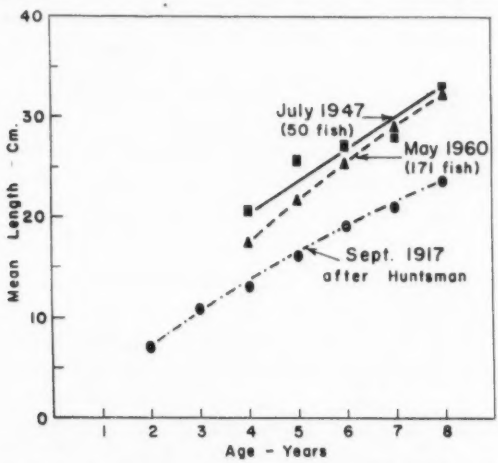


Fig. 7. Comparison between mean lengths-at-age of Magdalen Shallows plaice in 1917, 1947, and 1960. The 1917 and 1960 samples are from North Bay and the 1947 sample is from Chaleur Bay. Sexes have been combined.

ture fish for its marketable categories, but the majority caught during commercial fishing operations are immature (Powles, MS, 1964).

Little published material is available on the size at maturity of American plaice in other areas. Bagenal (1957), however, has investigated the breeding biology of the "long rough dab" (the European name for American plaice) in the Clyde area. There, the average maximum size is about 32 cm, and 50% of the female fish are mature by 19–21 cm in length (age 3). Huntsman (1918) suggests that plaice mature earlier in southern than in northern waters but no data were included for comparison.

Spawning

Figure 9B shows the spawning cycle of plaice and although samples were not obtained during all months, the percentage of fish in each reproductive phase gives a good indication of the spawning time. Half the fish in the samples spawned from the end of April to mid May. Duration of the spawning peak was short, since in February most of the plaice were still ripening, while nearly all were spent by June. Since fishing commences generally by the end of May, spawning has virtually been completed before fishing operations start. The end of April to mid May is somewhat earlier than the May–June period cited by Huntsman (1918), but is supported by the observations of Kennedy and Powles (MS, 1964). Bigelow and Schroeder (1953) state that the earliest

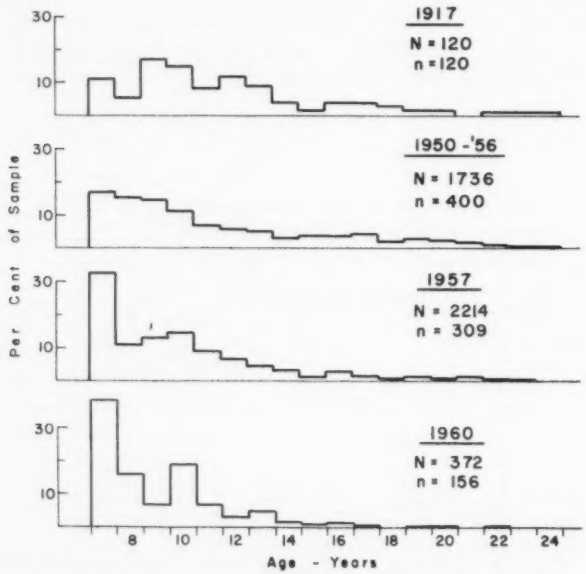


Fig. 8. Age composition of American plaice (sexes combined) from the Magdalen Shallows. The 1957 sample is from Shippegan Gully, the others from North Bay.

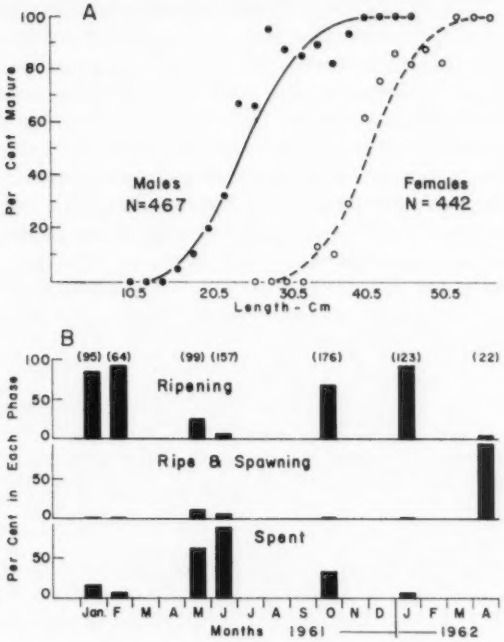


FIG. 9. **A.** The relationship of length to sexual maturity in American plaice from the Magdalen Shallows. **B.** The annual cycle of reproduction in plaice. The number of males and females (combined) in each monthly sample is shown in parentheses.

plaice eggs appeared in the Gulf of Maine in early March, but that spawning is not general until the last of March or first part of April. It spawns earlier in the North Sea than in American waters, i.e. from mid January to May, with the climax in March and April. Pitt (1963) has listed the probable spawning times of plaice for other localities in the northwest Atlantic.

FOOD STUDIES

MAJOR FOOD ITEMS AND COMPETITION. The distribution of American plaice parallels that of cod (Bigelow and Schroeder, 1953). In summer research hauls for plaice in the Magdalen Shallows area, cod were generally extremely abundant. Feeding data for plaice and cod are presented together in Fig. 10. It is clear that young plaice (under 30 cm) fed mainly on mysids, amphipods, small echinoderms and annelids. (The echinoderms taken by young plaice were principally the small brittle stars, *Ophiura sarsi* and *O. robusta*, and the annelids were smaller polychaete worms.) Cumaceans and other organisms were of lesser importance. Small cod took more euphausids and fish than

did small plaice, but they also ate substantial amounts of mysids, amphipods and decapod shrimps, all three of which are important plaice food.

Large plaice ate mainly echinoderms and pelecypods. Amphipods and polychaetes occurred less frequently, and volumetrically were less important than echinoderms and pelecypods. The most prominent echinoderms eaten by larger plaice were *Ophiopholis aculeata*, *Echinarachnius parma*, and *Strongylocentrotus droebbachiensis*. Pelecypods fed on were mainly *Yoldia myalis*, *Nuculana tenuisulcata*, *Clinocardium ciliatum*, and *Serripes groenlandicus*. Fish was only a minor part of the food taken by large plaice in this area. The food of large cod was less specialized than that of plaice, and large cod fed mainly on fish and crustaceans rather than echinoderms and molluscs. Nevertheless, appreciable food competition occurs between large cod and plaice for amphipods, mysids, decapods, and annelids.

Although food competition occurs between large plaice and cod, it is more marked among the smaller fish. Among larger fish, food competition is less keen because large plaice have a somewhat specialized diet. Furthermore, the specific organisms competed for by small plaice and cod are highly abundant forms in the area (Corbeil, 1954). It is therefore unlikely that food competition is a limiting factor for plaice, providing invertebrate abundance and composition remain stable.

SEASONAL CHANGES. Besides a pronounced change in food type with size, American plaice exhibited a rather striking seasonal variation in feeding intensity (Table I). Feeding was drastically reduced in the winter months of

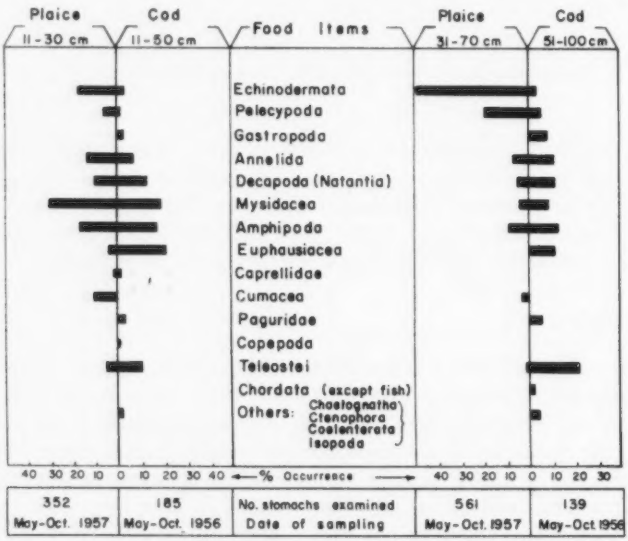


FIG. 10. Comparison of American plaice and cod feeding habits in the northern Magdalen Shallows. Percentages are based on the number of stomachs examined and the number of occurrences.

January and February, at which time 93% of the stomachs examined were empty. Among the few fish which did contain food, the mean volume of food was less than that observed during the summer and fall. No data were available for December and March in this area, but moderate feeding has been observed in November and April. The seasonal changes in feeding occurred among all sizes.

Such fluctuations in feeding intensity are common among the Heterosomata. Wimpenny (1949) states that European plaice feed most heavily from March to October, and that by November over 90% of the stomachs are empty.

Plaice Predation by Cod

Powles (1958) noted that large cod in the Magdalen Shallows feed heavily on fish. In 1956, plaice were volumetrically the second most important fish prey (after herring) in the stomachs of Atlantic cod. Because of its abundance and its similar distribution to plaice, cod is therefore an important predator of small plaice.

Combined food data for stations where cod and plaice occurred together during the summers of 1956–58 showed that the degree of plaice predation is positively correlated with the size of cod (Fig. 11). Cod were divided into six length groups (Fig. 11A) and the number of whole plaice in each cod stomach was recorded. Only 4% of the cod examined in the smallest category (42–53 cm) contained plaice, whereas 37% of the cod over 100 cm in length contained some plaice.

More than one plaice may be found in a single cod stomach at a particular time. The number of plaice per cod stomach was quite low in the smallest

Table I. Feeding intensity and mean volumes of food in stomachs of American plaice in the southwestern Gulf of St. Lawrence for three seasons, 1960–61.

Cruise		Size group (*cm*) 11–20	21–30	31–40	41–50	51–60	61–70	Total	Percentage empty
H-21 May–June 1960	No. examined	16	44	30	23	35	16	164	
	No. empty	0	3	2	1	3	0	9	5.5
	Mean volume[a] (*cc*[b]) (est.)	3.8	4.8	13.1	18.3	29.7	58.3		
H-27 Sept.–Oct. 1960	No. examined	45	48	48	9	2	0	152	
	No. empty	12	5	0	0	0	0	17	11.2
	Mean volume (*cc*) (est.)	1.2	4.8	9.9	21.7	27.5	–		
A-16 & 17 Jan.–Feb. 1961	No. examined	25	56	67	54	23	4	229	
	No. empty	24	52	61	51	21	4	213	93.1
	Mean volume (*cc*) (est.)	0.5	3.5	1.1	0.8	2.9	0.0		

[a]Mean volume represents mean only of stomachs containing food.
[b]Total volumes were estimated by eye and reduced to parts of 10 for each type of organism.

category of cod (0.04), but the number increased as the size of cod increased. Cod of 100 cm or more in length contained 0.5 plaice per stomach examined (Fig 11B).

Before the total instantaneous mortality of plaice due to cod grazing could be estimated, a number of assumptions had to be made. The most important was that the number of cod and plaice taken in any sample represented the same fraction of their total respective populations. In the present study the catches of many stations over a fairly large area were combined in an attempt to reduce errors due to inadequate sampling and spotty distribution.

To derive the grazing rate, one must know:

C_t = population of plaice-eating cod in the sample;

P_t = population of plaice subject to predation;

p_t = number of plaice found in cod stomachs;

Δ_t = time cod takes to digest a plaice;

g = instantaneous grazing mortality of plaice imposed by one cod.

Then $C_t g$ may be calculated from:

$$\frac{p_t}{P_t\ \Delta_t} = C_t g$$ = total instantaneous mortality due to cod grazing (for details, see Appendix 2).

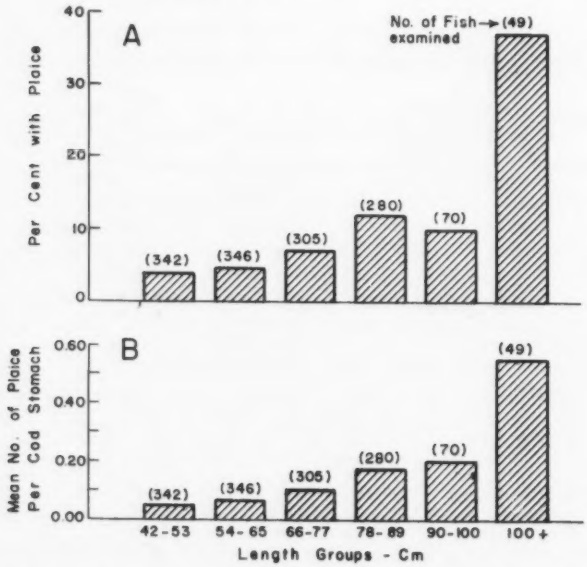


FIG. 11. **A.** Mean percentages of cod stomachs containing plaice by size group of cod. **B.** The mean numbers of plaice found in cod stomachs according to size of cod.

For estimations of the grazing rate, the amount of time required for one cod to digest a plaice meal was taken as 4–6 days. Data on this subject are scarce, but the choice of this period is based on the work of Karpevich and Bokova (1937; *also in* Zadulskaia and Smirnov, 1939) who investigated the digestion rate (of fish meals) of various species, including *Gadus callarias*. These authors started their investigations assuming a digestion period of 24 hr. Further investigations proved that the period was significantly longer, i.e. 5–6 days in the case of cod. The work of Saunders (1963) does not disagree with this, although it cannot be offered as direct supporting evidence. He found that the rate of oxygen consumption in Atlantic cod after a fish meal (herring) subsided to starvation level in 4–7 days, depending on temperature and amount of food eaten. At 10°C cod took 7 days to return to the previously established starvation level, and at 15°C, 4–5 days were required. Summer bottom temperatures in the Magdalen Shallows are generally lower than those in which the experiments were carried out (Fig. 16), and activity also probably differs in the natural habitat. The lower limit of 4 days was used because plaice may be digested beyond recognition by this time, and would not be identifiable.

The accuracy of the grazing rates presented here is open to question because knowledge of cod digestion rate under natural conditions is so limited. Also, grazing rate values are very sensitive to changes in Δ_t (the digestion rate), which may increase the scope for error. However, by using a constant period of time for Δ_t, relative differences in grazing rates between years are meaningful. More accurate computations will have to await special studies.

A second assumption made in the computations was that cod fed only on plaice 35 cm and smaller, estimated by observation only, since no accurate measurements of the prey are available.

Estimates of total instantaneous plaice mortality due to cod grazing in the northern sector were made for the years 1956–61 (Fig. 12A). These estimates were made by combining data from all stations. The upper limit is based on a 4-day digestion rate, the lower limit on a 6-day digestion rate. A downward trend in cod grazing is apparent from 1956 to 1961.

In some cases the predator–prey ratio affected the grazing values. However, there was no consistent trend. A positive correlation was found between the grazing rate and the mean size of cod (Fig. 12B), which was in turn proportional to the percentage of cod over 78 cm long (Fig. 12C). The abundance of large cod in the Magdalen Shallows has decreased markedly in the past decade (Jean, 1963), and this event has apparently also reduced the grazing rate on plaice.

It is impossible at present to consider the many other variables entering into the predator–prey relationship of cod and plaice, such as the abundance of other prey organisms, the effects of distribution, disease, and so on. The salient fact is that cod grazing showed a relative decrease in recent years which may favourably affect future plaice abundance.

Summer Distribution

Research cruises in the Magdalen Shallows showed that American plaice were taken on sand or sand-mud bottoms during May to October, principally between the depths of 40–200 m. No plaice was observed in the Northumberland Strait area, nor have young individuals been taken there by plankton nets or bottom drag (D.G. Wilder, personal communication). Rocky areas, such as those around Bonaventure Island and north and east of Prince Edward Island were generally unproductive for this species, although small numbers are occasionally landed from the latter region by line trawl.

Combining survey data from 1957 to 1960 showed that the heaviest summer catches (May–October) occurred inshore in Chaleur Bay, Shippegan Gully, and North Bay (Fig. 13). Large and small fish were found together at this time of the year. The distribution outlined in Fig. 13 is representative of most years (during 1957–61) except 1960, when research-vessel catches, commercial fleet concentration, and tagging results showed that plaice remained further offshore (see tagging section).

Seasonal Movements

In 1959 a series of stations (Fig. 15) was set up to investigate the extent and nature of seasonal movements. At various times of the year hauls were made across a range of depths and temperatures.

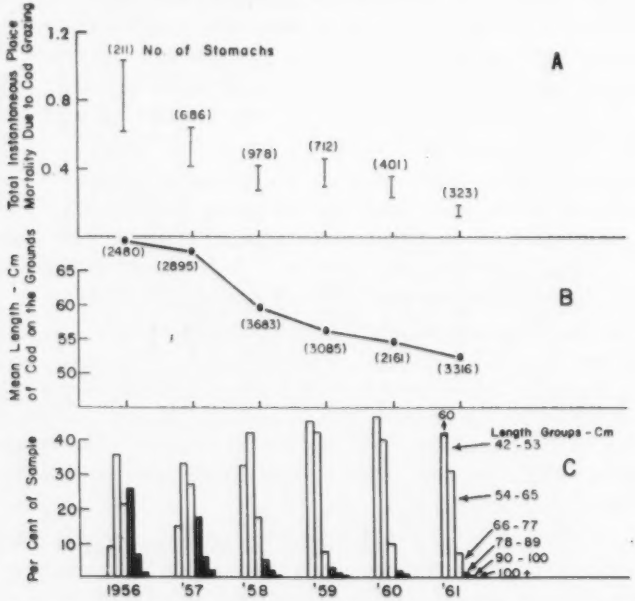


Fig. 12. The relationships between (A) cod grazing, (B) mean size of cod, and (C) relative abundance of large cod (dark bars) in the Magdalen Shallows, 1956–61.

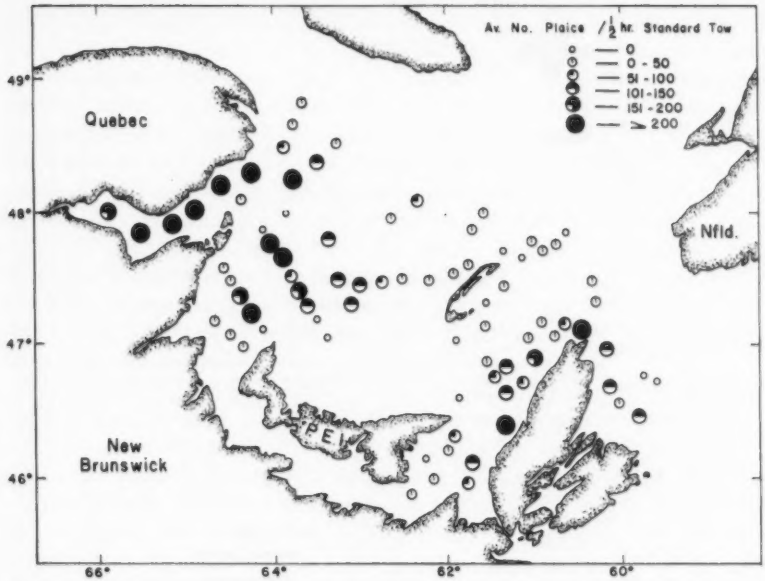


FIG. 13. The main centres of plaice distribution during the May–October period (composite of years 1957, 1958, and 1960) as shown by research-vessel surveys.

The abundance of American plaice in relation to depth and temperature ranges during four seasons is summarized in Fig. 14. Catches at similar depths and temperatures were combined and averaged for each cruise; the shallow depths generally represent inshore regions and the deeper ranges occur towards the Laurentian Channel. All sizes are included. In June, plaice were taken only at the inshore stations, between the depths of 40–100 m. Prevailing bottom temperatures ranged from −1.7 to 0.0°C, but most of the fish were taken in the higher limits of this range, i.e. −1.0 to 0.0°C. Plaice remained inshore during July, August, and September (not shown), but by October the largest catches were taken within the 75–146-m range where bottom temperatures were mostly 0.1–2.0°C. Maximum hauls in January were obtained further offshore, principally in the 185–457-m range, and bottom temperatures ranged from 2.1 to 5.0°C. In spring large catches of plaice were made from 75 to 146 m. Within the bottom temperature range of −1.7 to 5.0°C the largest catches occurred from 0.0–4.0°C.

Total catches do not present a complete picture of seasonal movements because sizes of fish are ignored. Seasonal differences in size and maturity occur, however, and are most marked in winter when it can be seen that the few fish remaining inshore are small immatures (Fig. 15, J,L,A). There were more small plaice (under 30 cm) in the deep water, but few under 20 cm long were found as far as the edge of the Laurentian Channel. The catches of mature fish increased with depth.

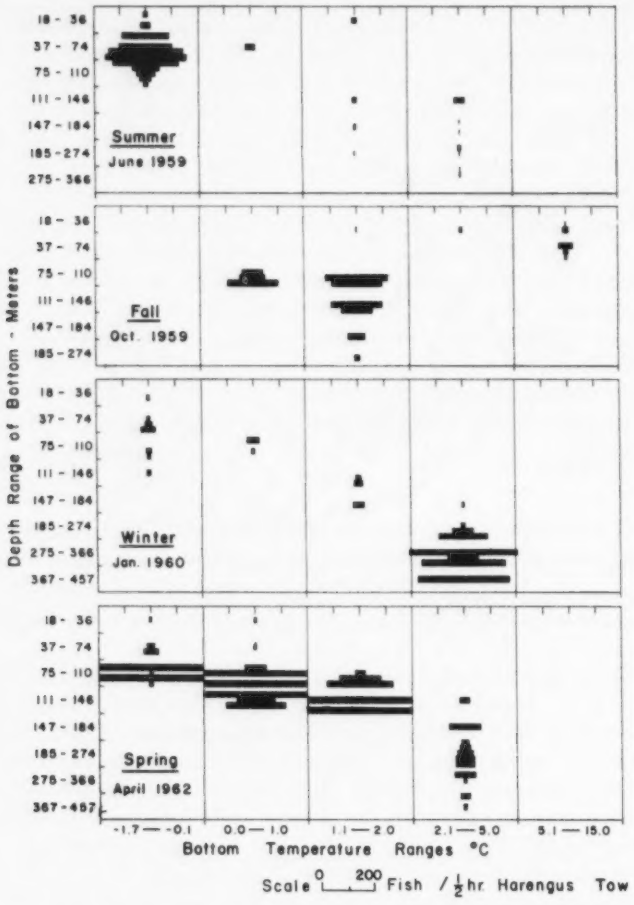


FIG. 14. Distribution of American plaice in relation to depth and temperature during the four seasons. Catches at similar depths are combined for each cruise and shown as mean number per ½-hr tow.

Individual hauls, together with ratios of immature to mature fish, during four research cruises are plotted in Fig. 16. Discounting annual variation, this diagram illustrates the seasonal environment of American plaice in the Magdalen Shallows, assuming they do not rise far off bottom. (The lines are the same as those of Fig. 15.) Feeding and reproductive biology may now be correlated with seasonal movements and environmental conditions of depth and temperature.

In early summer (Fig. 16, June, line LM and JK) both mature and immature plaice were found inshore in cool waters from 40 to 120 m. They had completed spawning by this time, and remained on the same grounds feeding

through July, August, and September. By October, the fish tended to move deeper and offshore (October, line LM, JK). Rapid rises in bottom temperature may initiate this movement. By October the cool bottom temperature at the first station of line L–M in June had increased to 7.0°C and only a few immature fish were present. All mature fish had migrated to deeper waters, and the gonads were beginning to ripen at this stage. By January, only a few immatures remained in the cold inshore waters, and the bulk of fish (and all mature fish) were found in warm deep water. Here they cease feeding, although the gonads continue to ripen. By early spring (April), plaice began moving inshore, and were taken over a wider temperature range (–1.0 to 5.0°C). This is just prior to spawning time, the gonads are ripe, and the fish begin feeding again. An individual fish moving inshore at this time would pass from warmer to cooler bottom temperatures.

This evidence contradicts the conclusions of Huntsman (1918) who wrote: "It [the plaice] perhaps moves to a slight extent toward the shore in the cold part of the year and away from it during summer, but this movement does not seem to be very distinct." However, he had no winter data for the area.

American plaice are not unique among flatfish in displaying seasonal movement. Milinsky (1944) discloses that "long rough dabs" (*Hippoglossoides platessoides*) in the Barents Sea make yearly east–west migrations to spawn. In the Pacific, mature petrale sole migrate as far as 350 miles to constant deep water areas (Alverson and Chatwin, 1957), and lemon sole (Ketchen,

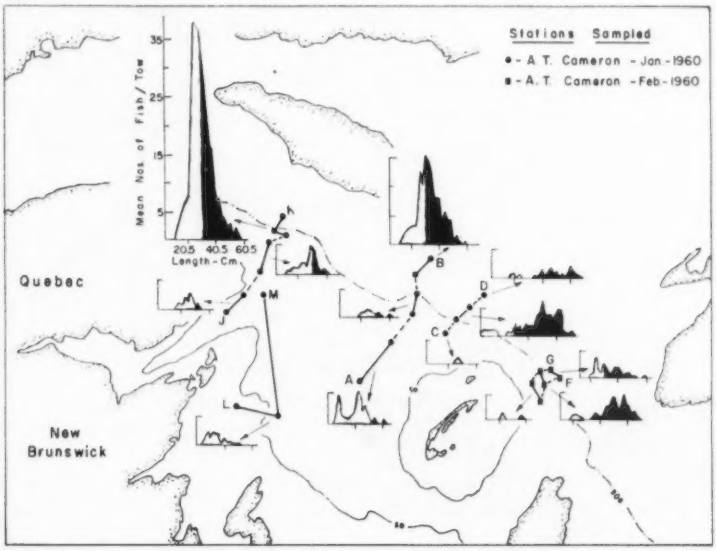


FIG. 15. Size and abundance of American plaice at various localities in the Magdalen Shallows in winter. Immature stages are white areas and stations of similar depth (joined by a solid line) are combined.

1956) and Dover sole (Hagerman, 1952; Harry, 1959) exhibit tendencies to migrate seasonally but on a lesser scale. In the Atlantic, the yellowtail flounder off New England shows annual migrations of distances up to 200 miles (Royce

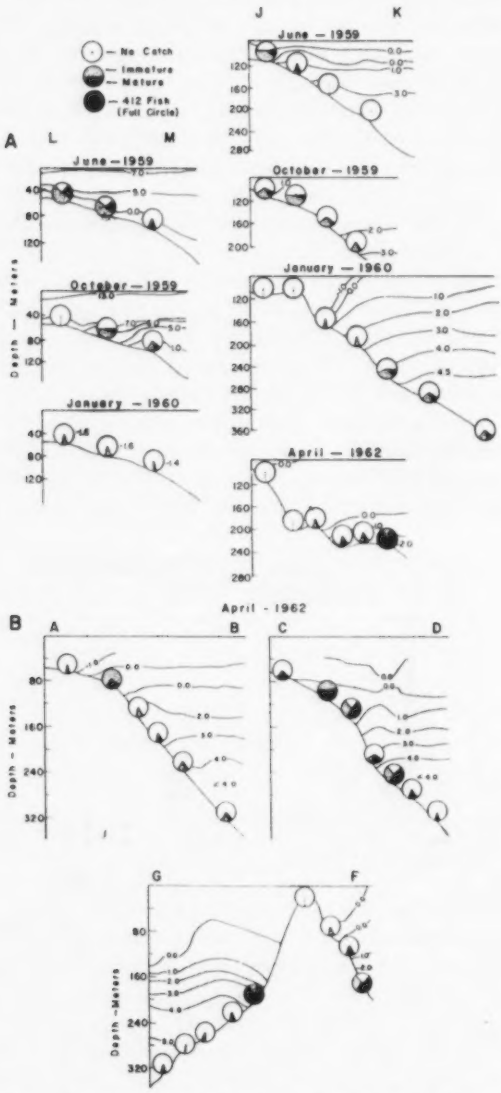


FIG. 16. The number of plaice taken at each station per ½-hr standard tow during various seasons together with the observed depths and temperatures. The sections are the same as those shown in Fig. 15.

et al., 1959), and in the St. Mary Bay area, Nova Scotia, winter flounders leave the Bay for deeper waters in winter (McCracken, 1963).

The exact mechanisms involved and the factors responsible for the movements of plaice in the Magdalen Shallows have not been studied, but it is apparent that seasonal migrations enable them to avoid the extremely cold bottom temperatures which would be encountered during the winter.

DIVISION OF STOCK

Tagging Experiments

In 1958, tagging experiments were begun to obtain data on growth and movements. Each lot of tagged plaice was given a number for ease of reference. The number of fish tagged, the release areas, and corresponding dates are shown in Fig. 17. In 1958 and 1959, plaice were tagged in Shippegan Gully, at the mouth of Chaleur Bay, in "North Bay" (a local term for the area off Cheticamp), in Chaleur Bay, and around Orphan Bank. In 1960 a number of plaice was tagged on the Magdalen Islands Banks. All individuals in this lot (#6, Fig. 17) were old, mature fish. In earlier years heavy landings of such fish were made from the same area, but large concentrations have not been reported since 1955. Tagging was thus carried out near the centres of the

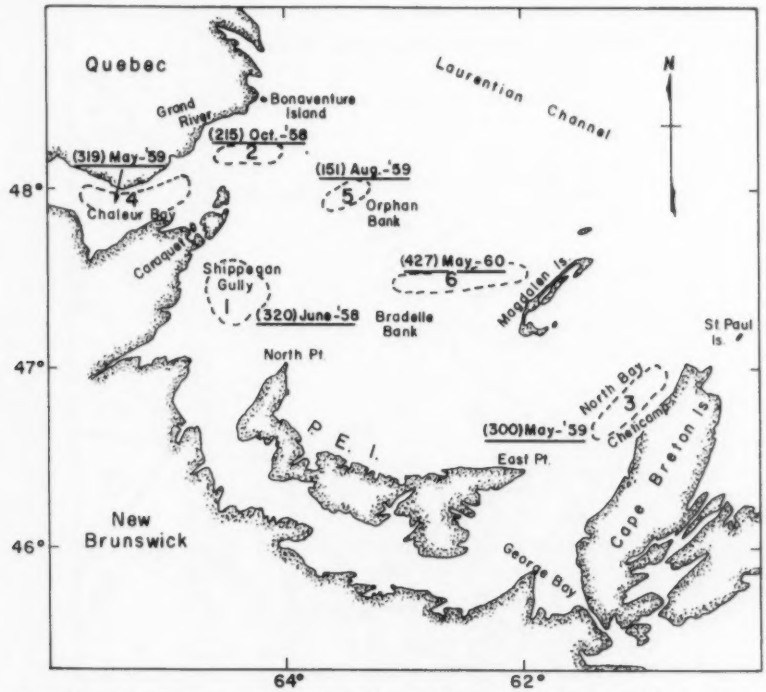


FIG. 17. Tagging areas, dates, and numbers of American plaice tagged from 1958 to 1960. Dotted lines enclose the lot number and outline the release areas.

most active fishing areas, and lots 1, 3, 4, and 6 were tagged during or just after the spawning season.

Of 1732 flounder marked from 1958 to 1960, 668 (39%) were returned during the 1958–61 period. Of these, 425 (25%) gave reliable recapture location. Area information for the remaining 243 was either unknown, unreliable, or the recoveries were made in processing plants. Several old fish moved distances of about 100 miles, and one was recaptured 150 miles away, but most plaice were retaken within a radius of 60 miles from their release areas.

The interpretation of tagging results to determine seasonal movements is difficult for two reasons. The first was that, during winter, fishing virtually ceases in the Magdalen Shallows (ICNAF Division 4T) except for a few large vessels fishing from the Magdalen Islands to Cape Breton in deep water. This made the probability of winter recaptures slight from the northern part of the Magdalen Shallows. Secondly, in spring and late fall tags could not always be collected immediately by research technicians, and consequently, accurate area information was frequently lost.

Commercial plaice catches by groundfish unit areas (Fig. 18), from log records of the Fisheries Research Board of Canada, revealed that some plaice fishing was carried out in nearly all areas during the fishing season (Table II).

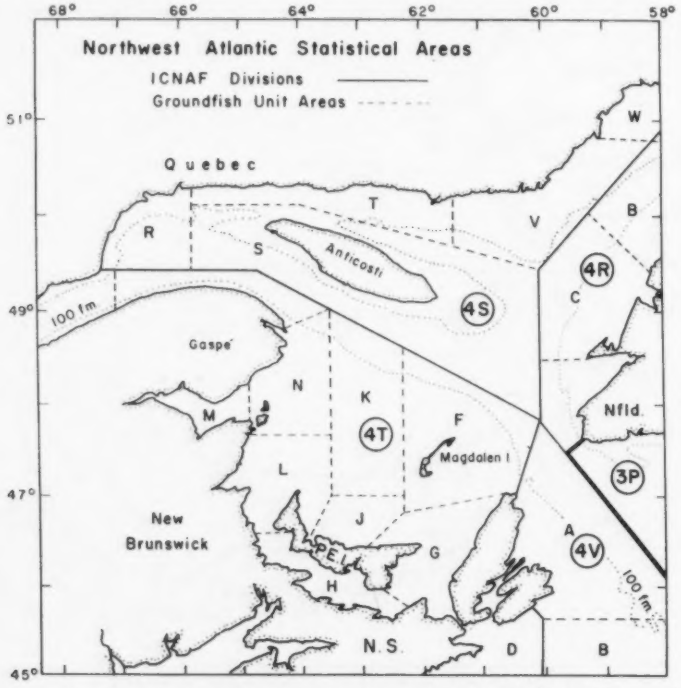


FIG. 18. Map showing the Gulf of St. Lawrence with ICNAF divisions and statistical unit areas.

TABLE II. Average plaice landings (lb) for 1959–61 by month and groundfish unit area as recorded by the offshore fleet. About 50% of the total fleet fishing in the Magdalen Shallows (ICNAF Division 4T) record their catches in special log books provided by the Fisheries Research Board of Canada.

Regions within ICNAF Div. 4T	Groundfish unit area	May	June	July	August	Sept.	Oct.	Nov.	Dec.
Chaleur Bay	M	–	71,900	127,200	194,500	174,200	223,400	236,900	–
Orphan Bank	N	102,000	205,000	227,400	242,500	167,600	104,600	157,000	–
Shippegan Gully	L	55,400	170,800	164,100	208,100	142,200	125,700	74,500	1,500
Bradelle Bank	K	62,400	59,500	31,100	37,200	22,200	87,900	120,600	7,000
Prince Edward Island	J	No landings							
Magdalen Islands	F	200,900	282,500	154,400	34,300	53,400	108,300	58,600	201,900
North Bay	G	500,100	1,175,600	665,700	454,000	302,600	380,400	579,100	370,100

The tagging data therefore provide useful estimates of the extent of mixture between regions, but are somewhat less useful for the determination of seasonal movements.

Several points are brought out by the data of Table II, and these support conclusions already reached concerning seasonal movements. For example, fishing did not start in Chaleur Bay (i.e. inshore) until June and lasted only until November. In the offshore regions of Bradelle Bank and Magdalen Islands, peak landings were in early summer and fall. The important points concerning stock delineation, however, are the following: (1) the middle areas K and J (Fig. 18) support little or no fishing compared to the northwest and southeast regions of the Magdalen Shallows; (2) in spite of a substantial fishery in the North Bay area, the only plaice tagged north of Prince Edward Island and recaptured in North Bay were several old fish from the Magdalen Banks (Fig. 20); (3) likewise, no fish tagged in North Bay was retaken north of P.E.I. in spite of the active fishery in Chaleur Bay, Shippegan Gully, and Orphan Bank.

Most of the returns from the 1958 tagging occurred close to the release areas; there was moderate mixing between areas 1 and 2, and a few fish were retaken in Chaleur Bay (Fig. 19). In 1960 fewer lot 1 recoveries occurred in the release area than in 1959 or 1961. Two distant recaptures (over 50 miles from release point) were made from the Laurentian Channel in spring (Fig. 19C, D).

The pattern of recaptures for lots 3–6 in 1959 and 1960 was more diverse (Fig. 20). From lot 4 (Chaleur Bay), most tags in 1959 were returned from the release area during the summer months in spite of extensive fishing outside the Bay (Table II, area N). By fall, however, one-third of the recaptures were from outside the Bay (Fig. 20A). The following spring seven were retaken outside the Bay, but during the summer, recaptures were again inside the Bay (Fig. 20B). Since tag returns usually reflect fleet and fish distribution, these data suggest a late fall exodus from, and a spring entry into, the Bay of Chaleur.

Lot 5 (Orphan Bank) fish showed little tendency to spread, and returns appeared mainly in the Orphan–Bonaventure region (Fig. 20A, B, C). Returns from lot 3 (North Bay) similarly showed little dispersion. A number of tags was recaught in the Laurentian Channel region, but most recaptures were in the release area. No tags were retaken north of the Magdalen Islands.

The recapture pattern of lot 6 (Magdalen Banks) plaice clearly suggests a considerable amount of movement (Fig. 20B, C). Returns in 1962 and 1963 (not shown) also indicate extensive wanderings by these older fish. During the summer of 1960, 15 returns were from the release area and one from Chaleur Bay. Two were retaken in the Laurentian Channel in fall (Fig. 20B). In 1961 early summer recaptures were from the release area and Laurentian Channel, followed later by returns from the entrance to Chaleur Bay and Shippegan Gully (Fig. 20C). Another summer recapture was made off P.E.I. by a longliner, while all fall and winter returns were to the east in deep water.

Large, discrete aggregations of old plaice have become uncommon in recent years. Fishermen used to report them occasionally from Chaleur Bay, Miscou, Magdalen, and Sable Island Banks, and many fishermen considered them a separate species of flounder. During surveys from 1957 to 1961 only remnants of such aggregations were encountered — on the Magdalen Banks and in Sydney Bight. Most fish were over 16 years of age, and 30% were over

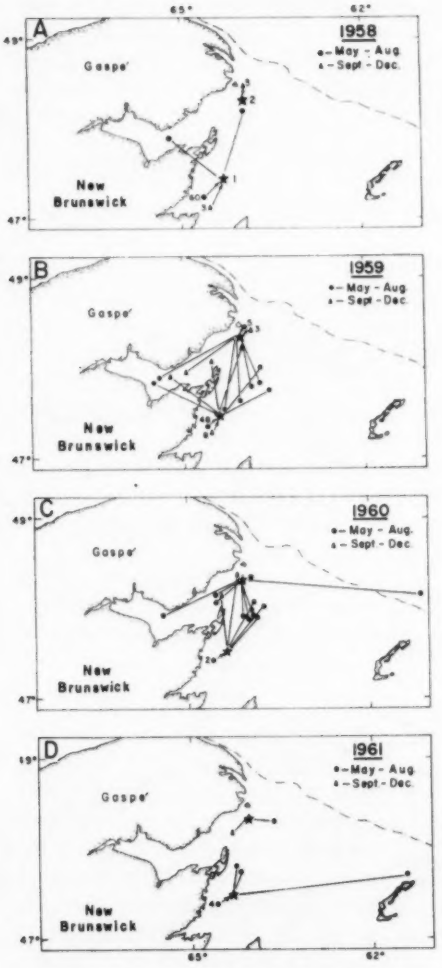


FIG. 19. Recaptures of tagged plaice, lots 1 and 2. Circles and triangles represent individual fish, while numbers returned within the release area (star) are denoted by arrows.

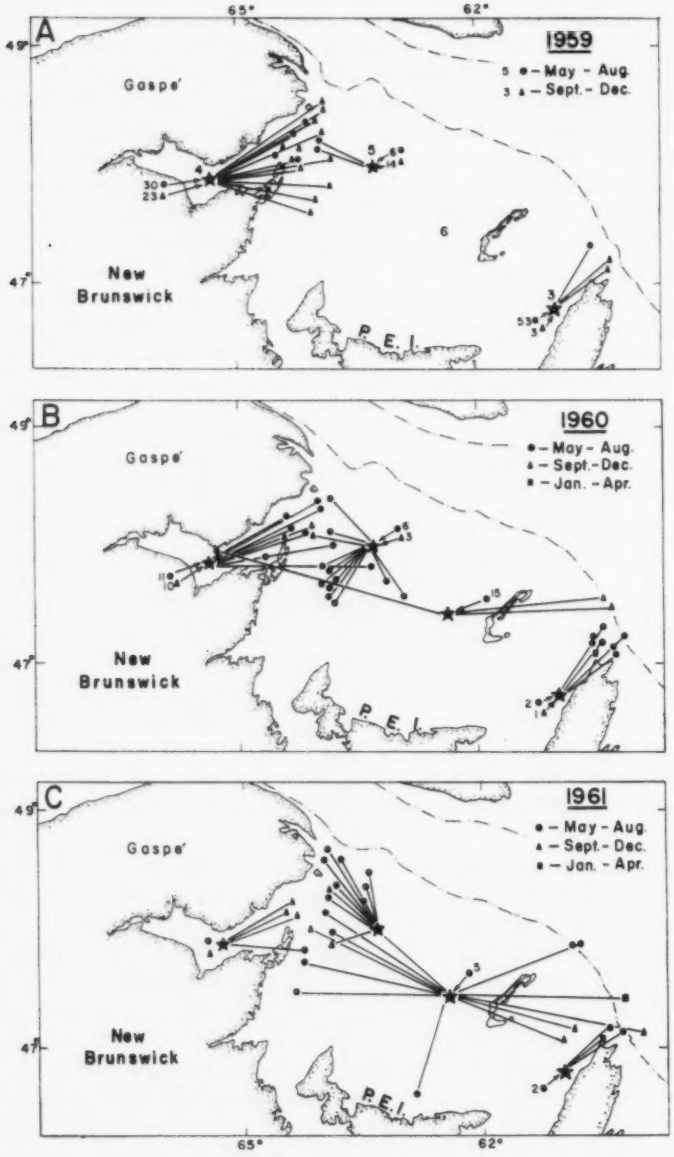


FIG. 20. Recaptures of tagged plaice, lots 3–6, inclusive. Symbols are explained in Fig. 19.

20. While such old fish (typified by lot 6) moved around extensively, they are only a small fraction of the total stock by number.

Tagging experiments in 1963 in the George Bay area (Powles, unpublished data) indicated extensive mixture between tag lots in the southern part of the Magdalen Shallows (North Bay). None of these tags has been retaken yet in the so-called northern sector.

The main points arising from the tagging data are: (1) intermixing occurred between all lots in the area north of P.E.I. (northern sector); (2) except for a few older individuals, fish tagged in the northern sector were not retaken in the southern sector (George Bay–St. Paul Island) and vice versa; (3) the majority of summer recaptures were close to their release (spawning) areas each year; (4) early-spring, fall, and winter returns came from deeper waters to the east, i.e. where the fishery was most active; (5) no emigration occurred far outside the Magdalen Shallows.

Meristic Studies

While the chief method of determining the extent of mingling between areas was tagging, some counts of anal fin rays were analysed (Fig. 21). Since no significant differences between sexes were observed, counts for both sexes were combined. The fin-ray counts were analysed and compared by means of Fisher's *t*-test (Snedecor, 1956).

Figure 21 shows that the magnitude of the means of each sample increased gradually in a southerly direction. The difference between the Orphan and Scatari Bank samples was significant at the 0.01 level. The Scatari Bank sample also differed from all three samples within the Magdalen Shallows at the 0.05 level, while no difference existed between any of the latter three areas.

These results corroborate earlier conclusions reached from the tagging studies and are supported by the findings of Pitt (1963), whose vertebral studies indicated that Magdalen Shallows plaice were biologically discrete.

Stock Delineation

The Magdalen Shallows stock, although biologically discrete, is made up of two groups: the northern ("Miscou–Magdalen") group and the southern ("Cape Breton") group. These "groups" (Marr, 1957) are not separable by meristic characters, probably because of larval drift since there is little mixing of adults. The northern group is distributed within Chaleur Bay and the area bounded by Orphan Bank, North Point, Prince Edward Island, and the Magdalen Islands. The two main centres of distribution in summer are in Chaleur Bay and in the area from Shippegan Gully to Orphan Bank. In late fall the fish move eastward towards the Laurentian Channel into deep water where they remain during the months of January–March. A few immature fish remain inshore. By the end of March, plaice begin to leave deep water and in April they are at intermediate distances between their winter and summer

grounds. A small fraction of the group, made up of large post-spawners, may remain feeding on the Magdalen Islands Banks in aggregations until June. These older fish may wander extensively but the rest of the fish generally move inshore by late May in the Shippegan region, and early June in the Chaleur Bay region. Large, discrete concentrations of very old plaice occurred in 1950, 1954, and 1955 (years which also correspond to successful broods), but in the past decade very old fish have become scarce.

The "Cape Breton" group is spread between the Magdalen Islands and Cape Breton, from George Bay east to St. Paul Island. Seasonal movements are similar to, but less extensive than, those observed in the northern group because the fish are closer to deep water. Fishing is carried out over a wider season, beginning in May and continuing into December and January under favourable conditions.

The delineation of the Magdalen Shallows stock and the biological characteristics of the two main groups of plaice will greatly facilitate future considerations of the fishery. The seasonal activities and distribution of each group will aid in visualizing the mechanics of both the fishery and the natural population. Since the two groups differ somewhat in age composition and sex ratio, it will now be possible to compute sustained yields more accurately by treating each region separately.

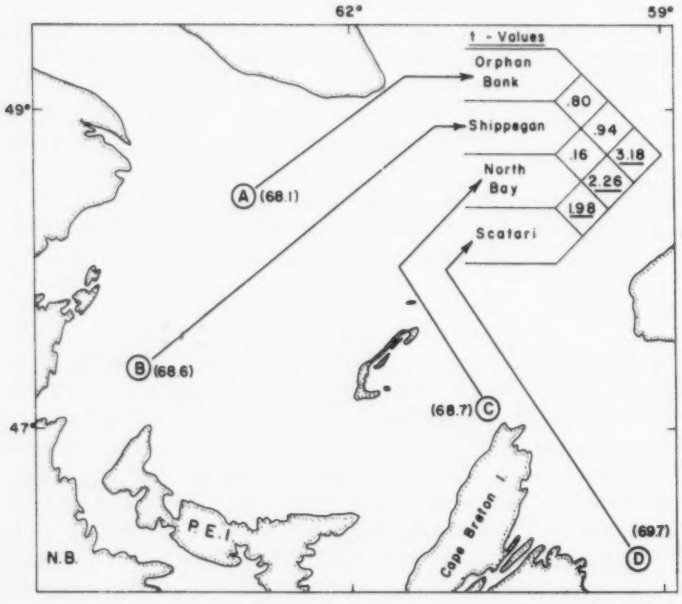


FIG. 21. Anal fin-ray sampling localities together with *t*-values obtained from comparisons between areas. Significant differences ($P > 0.05$) between samples are underlined. The average fin-ray count for each locality is shown in parentheses.

SUMMARY

1. The American plaice is a common sub-arctic flounder distributed from Cape Cod to Labrador. In the Magdalen Shallows (ICNAF Division 4T) the species is taken in considerable quantity, principally along with Atlantic cod.
2. In the Magdalen Shallows, plaice of both sexes grow at the same rate until age 4 when they are roughly 20 cm long. Thereafter, female plaice grow more rapidly, reaching commercial size (32 cm) by age 8, compared to age 10 for males.
3. The growth rate of Magdalen Shallows plaice is similar to that of Labrador plaice, but is much slower than that for plaice found off Cape Cod. Longevity of *Hippoglossoides platessoides* is greater in American waters than it is around Scotland and Iceland.
4. The 1950, 1953, and 1954 year-classes were strong in survey catches sampled from 1957 to 1961.
5. Growth rate is now more rapid than in the time of Huntsman's sampling (1917), but has remained uniform during the period 1947–60.
6. Data from various sources in 1917, 1950, 1957, and 1961 suggest that the mean age and size have changed, becoming younger and smaller in later years.
7. Female plaice attained first maturity at 30 cm, but 50% were not mature until age 10 (41 cm). On the other hand, 50% of the males were mature at 25 cm in length (age 6).
8. Maximum spawning occurred from mid April to mid May.
9. Competition for specific food items between plaice and cod was most marked among young fish. No competition was evident between small and large plaice, since the young fed primarily on polychaetes and small crustaceans, whereas large plaice ingested echinoderms and molluscs. Feeding of plaice decreased in intensity during January to March, inclusive.
10. Predation of small plaice by cod was investigated for the years 1956–61. The main predators were cod over 78 cm long, and the prey, plaice, mainly less than 35 cm. The observed decrease in mortality of plaice due to cod grazing in recent years was attributed to declining numbers of large cod.
11. Plaice migrated in late fall from inshore summer feeding grounds (40–110 m) to deep water along the Laurentian Channel. The best winter catches were made from 185 to 457 m, where bottom temperatures were 3–6°C. In spring, plaice were found at intermediate depths of 75–150 m over a wide temperature range (–1.7 to 5.0°C). Small numbers of "immatures" were the only plaice taken in the cold inshore waters during winter.
12. Three main centres of summer distribution were in Chaleur Bay, Shippegan Gully, and North Bay.

13. Tagging studies disclosed extensive mixing between Chaleur Bay and Shippegan Gully plaice, but no mixing between the northern and southern sectors of the Magdalen Shallows except for a few very old individuals.
14. No significant difference in anal fin-ray counts was observed between three sampling areas within the Magdalen Shallows. However, a Scatari sample differed from all three Magdalen samples at the 0.05 level.
15. The Magdalen Shallows stock of American plaice was biologically discrete, but was made up of two main groups. The two groups were named "Miscou–Magdalen" or northern group, and "Cape Breton" or southern group.

ACKNOWLEDGMENTS

I am indebted to Dr F. D. McCracken, head of the groundfish investigation at this Station, for his helpful suggestions in developing this publication from portions of my thesis.

Drs Alexandre Marcotte and Paul Montreuil both made unpublished plaice data available, and the former provided samples and working facilities at the Station de Biologie marine, Grande-Rivière, Que. Mr Fred Lux, U.S. Fish and Wildlife Service, Woods Hole, Mass., kindly provided a sample of plaice otoliths from the Cape Cod region.

I wish also to record with thanks the names of various staff members of this Station who rendered valuable assistance: Messrs McMullon and Cunningham produced most of the figures; Mr D. N. Fitzgerald summarized the commercial log records; Messrs Cadima and Paloheimo gave advice on computing cod grazing rates; and Drs Martin, Jean, and Kohler made available data from their research cruises.

REFERENCES

ALVERSON, D. L., AND B. M. CHATWIN. 1957. Results from tagging experiments on a spawning stock of petrale sole, *Eopsetta jordani* (Lockington). *J. Fish. Res. Bd. Canada*, **14**(6): 953–974.

BAGENAL, T. B. 1955. The growth rate of the long rough dab, *Hippoglossoides platessoides* (F.) — a correction. *J. Mar. Biol. Ass. U.K.*, **34**: 643–647.
1957. The breeding and fecundity of the long rough dab, *Hippoglossoides platessoides* (F.) and the associated cycle in condition. *Ibid.*, **36**: 339–375.

BERTALANFFY, L. VON. 1938. A quantitative theory of organic growth. *Human Biol.*, **10**(2): 181–213.

BIGELOW, H. B., AND W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. (First Revision). *U.S. Fish Wildlife Serv., Fish. Bull.*, **53**: 1–577. (Fish. Bull. No. 74)

CORBEIL, H.-E. 1954. Inventoire de la faune benthique des bancs de pêche. *Contr. Dépt. Pêcheries, Québec*, No. 43, pp. 13–18.

FINNEY, D. J. 1952. Statistical methods in biological assay. Charles Griffin, Co. London, 2nd ed. 661 pp.

FISHER, R. A., AND F. YATES. 1943. Statistical tables for biological, agricultural and medical research. Oliver and Boyd, Ltd., London, 2nd ed. 98 pp.

FLEMING, A. M. 1960. Age, growth and sexual maturity of cod (*Gadus morhua* L.) in the Newfoundland area, 1947–1950. *J. Fish. Res. Bd. Canada*, **17**(6): 775–809.

HACHEY, H. B. 1961. Oceanography and Canadian Atlantic waters. *Bull. Fish. Res. Bd. Canada*, No. 134, 120 pp.

HAGERMAN, F. B. 1952. The biology of the Dover sole, *Microstomus pacificus* (Lockington). *California Dept. Fish Game, Bureau Marine Fisheries, Fish. Bull.* No. 85.

HARRY, G. Y., Jr. 1959. Time of spawning, length at maturity and fecundity of the English, petrale and Dover soles. *Oregon Fish. Comm. Res. Briefs*, **7**(1): 5–13.

HUNTSMAN, A. G. 1918. Histories of new food fishes. 1. The Canadian plaice. *Bull. Biol. Bd. Canada*, No. 1, 32 pp.

JEAN, Y. 1963. Discards of fish at sea by northern New Brunswick draggers. *J. Fish. Res. Bd. Canada*, **20**(2): 497–524.

KARPEVICH, A., AND E. BOKOVA. 1937. The rate of digestion in marine fishes. [Russian; English summary]. *Zool. Zhur.*, **16**: 28–44.

KENNEDY, V. S., AND P. M. POWLES. MS, 1964. Plankton collections from the western Gulf of St. Lawrence and central Nova Scotian Banks, 1958–1962. *Fish Res. Bd. Canada, MS Rept. (Biol.)*, No. 799, 69 pp.

KETCHEN, K. S. 1956. Factors influencing the survival of the lemon sole, *Parophrys vetulus*, in Hecate Strait, British Columbia. *J. Fish. Res. Bd. Canada*, **13**(5): 647–694.

KOHLER, A. C., AND J. R. CLARK. 1958. Haddock scale-otolith comparisons. *J. Fish. Res. Bd. Canada*, **15**(6): 1239–1246.

LANULOV, K. P. 1962. Age and growth of the American plaice in the northwest Atlantic. Soviet Fisheries Investigations in the Northwest Atlantic (Y. Y. Marti, ed.). [Israel Program for Scientific Translations, Jerusalem, 1963].

LAUZIER, L. 1957. Report of the Atlantic Herring Investigation Committee. Section 10. Effect of storms on the water conditions in the Magdalen Shallows. *Bull. Fish. Res. Bd. Canada*, No. 111, pp. 185–192.

LUX, F. E. 1960. Length shrinkage of yellowtail flounder between live and landed condition. *Trans. Amer. Fish. Soc.*, **89**(4): 373–374.

MCCRACKEN, F. D. 1957. Results of cod tagging off eastern Nova Scotia. *Fish Res. Bd. Canada, Atlantic Prog. Rept.*, No. 67, pp. 6–13.

1963. Seasonal movements of the winter flounder, *Pseudopleuronectes americanus* (Walbaum), on the Atlantic coast. *J. Fish. Res. Bd. Canada*, **20**(2): 551–586.

MANZER, J. I., AND F. H. C. TAYLOR. 1947. The growth rate of the lemon sole in the Strait of Georgia. *Fish. Res. Bd. Canada, Pacific Prog. Rept.*, No. 72, pp. 24–27.

MARR, J. C. 1957. Contributions to the study of subpopulations of fishes. [Co-ordinated by J. C. Marr.] *U.S. Fish Wildlife Serv., Spec. Sci. Rept., Fish.*, No. 208.

MILINSKY, G. I. 1944. On the biology and fisheries of the long rough dab of the Barents Sea. *Trudy Poliarnogo N.-I. Instituta Morskogo Rybnogo Khoziaistva i Okeanografii imeni N.M. Knipovicha (PINRO)*, **8**: 388–415. [Russian; English summary]

PITT, T. K. 1963. Vertebral numbers of American plaice, *Hippoglossoides platessoides* (Fabricius), in the northwest Atlantic. *J. Fish. Res. Bd. Canada*, **20**(5): 1159–1181.

POWLES, P. M. 1958. Studies of reproduction and feeding of Atlantic cod (*Gadus callarias* L.) in the southwestern Gulf of St. Lawrence. *J. Fish. Res. Bd. Canada*, **15**(6): 1383–1402.

MS, 1964. Some factors affecting stocks and landings of American plaice (*Hippoglossoides platessoides* F.) in the southwestern Gulf of St. Lawrence. Ph.D. thesis, McGill University, Montreal, 172 pp.

RICKER, W. E. 1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Bd. Canada*, No. 119, 300 pp.

ROYCE, W. F., R. J. BULLER, AND E. D. PREMETZ. 1959. Decline of the yellowtail flounder (*Limanda ferruginea*) off New England. *U.S. Fish Wildlife Serv., Fish. Bull.*, No. 146, pp. 169–267.

SAEMUNDSSON, B. 1925. Fiskirannsoknir 1923–24. Andvari, Reykjavik, pp. 33–71.

SAUNDERS, R. L. 1963. Respiration of the Atlantic cod. *J. Fish. Res. Bd. Canada*, **20**(2): 373–386.

SIMPSON, G. G., C. S. PITTENDRIGH, AND L. H. TIFFANY. 1957. Life. Harcourt, Brace and Co., 1st ed. 845 pp.

SNEDECOR, G. W. 1956. Statistical methods. Iowa State College Press, 5th ed., 534 pp.

STEELE, D. H. 1957. The redfish (*Sebastes marinus* L.) in the western Gulf of St. Lawrence. *J. Fish Res. Bd. Canada*, **14**(6): 899–924.

WALFORD, L. A. 1946. A new graphic method of describing the growth of animals. *Biol. Bull.*, **90**(2): 141–147.

WIMPENNY, R. S. 1949. The plaice. Edward Arnold and Co., London.

ZADULSKAIA, E. S., AND K. S. SMIRNOV. 1939. Sutochnyi khod pitaniia treski v promyslovykh raionakh Barentsova moria. [Diurnal pattern of feeding of cod on the fishing grounds of the Barents Sea.] *Trudy Vsesoiuznogo N. I. Instituta Morskogo Rybnogo Khoziaistva i Okeanografii*, **4**: 321–338. [Fish. Res. Bd. Canada, Translation Series No. 483]

APPENDIX 1

Description of reproductive phases in American plaice used in this study. Male stages in the cycle were limited to four because of the difficulty in interpreting the cycle by gross examination (naked eye).

Females

1. *Immature* — ovaries transparent or translucent; red or pink in colour; generally not exceeding 40 mm in length.

2. *Ripening* — ovaries orange or containing small opaque eggs visible to the naked eye; will spawn the following calendar year; ovary length 40–50 mm.

3. *Ripe* — ovaries larger and pink to white in colour, containing some transparent eggs; will release some eggs on pressure exertion and will spawn very shortly; ovaries usually exceed 60 mm in length.

4. *Spawning* — as above but with patches of transparent eggs throughout and in the lumen; eggs flow without pressure.

5. *Spent* — ovaries flaccid, purplish to red in colour, usually empty but a few eggs may remain inside — long and thin compared to 4.

6. *Recovering* — ovaries intermediate in size, similar to 2 — ripening, pink to grey but never transparent; will include fish which have spawned the previous year but will not spawn during the year of sampling.

Males

1. *Immature* — testes clear or translucent, not extending into abdominal cavity.

2. *Ripening* — testes white and full, extending anteriorly into abdominal cavity; will probably spawn next year.

3. *Ripe and/or spawning* — full, milt running out easily; includes partly spent fish with upper testes partly in spent condition.

4. *Spent-recovering* — red-brown to greyish-brown and not full as in 3; may extend a little into abdominal cavity; will include fish in which upper testes spent, while lower may still be ripe or running.

APPENDIX 2

Calculation of total instantaneous plaice mortality due to cod grazing. The fraction of plaice grazed upon by cod may be calculated if one knows the ratio between plaice ingested and total plaice on the grounds at any one time. This requires only the simple computations shown in Appendix Table I.

The plaice present in stomachs of cod, however, may have already been there for some time prior to ingestion. This time is dependent on the rate of digestion of cod. Temperature is one of the main factors influencing digestion rate, while others, such as activity, crowding, and spawning condition may lengthen or shorten the time required for digestion. Further experimental work will be necessary to refine such investigations, but no attempt has been made here to adjust for various factors. The limits of cod digestion rate were set at 4–6 days, but the most likely levels of cod grazing rates within this range cannot be determined at present.

Cod predation on plaice can be considered to occur only during the time that the two species come in direct contact, i.e. during the summer months, June–September, or approximately 123 days. Cod move into the northern sector in May, and move out in October (A.C. Kohler, personal communication). During November–April they tend to be distributed from the Magdalen

APPENDIX TABLE I. Sample computation of the fraction of plaice eaten by cod. The data are for five stations in the northern sector of the Magdalen Shallows, 1957.[a]

1	2	3	4	5	6	7	8
Cod length group	No. cod stomachs examined	No. plaice found	No. plaice eaten/cod	Total cod caught C_t	Total plaice eaten p_t	Total plaice caught (under 35 cm) $P_t + p_t$	Fraction of plaice grazed upon by cod in time t
cm							
54–65	173	4	0.023	465	11		
66–77	158	8	0.052	437	23		
78–89	108	13	0.120	302	36		167/10862
90–100	48	20	0.417	133	55		
101 +	35	13	0.372	112	42		
	522	58		1449	167	10862	0.0154

[a]Column 3 shows the number of plaice found in the cod stomachs of column 2. Column 4 is the number of plaice eaten per cod during time t. Column 5 (C_t) represents the population of plaice-eating cod in the locality where the sample was taken. Only cod over 50 cm in length were considered here. Column 6 is the product of columns 4 and 5, and represents the number of plaice which would be eaten by the cod on the grounds (C_t). The total number of prey on the same grounds is shown in column 7. Only those plaice under 35 cm in length make up the prey of cod.

Islands to Sydney Bight, and are then in contact with the marginal portions of the southern group of plaice.

The period of contact between species must be adjusted by the digestion rate to obtain the total instantaneous plaice mortality due to cod grazing during this time. The limits placed on the digestion rate were 4 and 6 days. The fraction 0.0154 (see Appendix Table I) now becomes:

$$\text{upper limit } 0.0154 \times \frac{123}{4} = 0.477 = \text{total instantaneous plaice mortality due to cod grazing;}$$

$$\text{lower limit } 0.0154 \times \frac{123}{6} = 0.308 = \text{total instantaneous plaice mortality due to cod grazing.}$$

Bay of Islands and Humber River Atlantic Salmon Investigations[1]

By A. A. Blair

Fisheries Research Board of Canada
Biological Station, St. John's, Nfld.

ABSTRACT

Humber River is one of the important Atlantic salmon rivers of Newfoundland both from the standpoint of the angling in the river and the commercial fishery at the mouth of the river in Bay of Islands. The fishery was investigated in 1942 and a general survey was made of the main river and its tributaries in 1943 to determine conditions for spawning.

The sea-age classes of Bay of Islands salmon and their percentage composition were: 1, 57.2; 2, 32.8; 3, 0.5; and previously spawned, 9.5. The 1 sea-year or grilse class was less numerous in June than 2 sea-year class, but was more numerous during the rest of the season. The 3 sea-year class was not represented at all until August, whereas the previously-spawned class had a higher representation in the first half of June than it did later in the season. According to fishermen's reports, the time of the run of the older salmon is usually from the last week of May to the first week of August with the peak around June 15, whereas grilse are caught from June 15 to the last week in August with the peak during the first half of July.

The river-age classes of Bay of Islands salmon and their percentage representation were: 2, 2.1; 3, 42.1; 4, 51.6; 5, 4.0; and 6, 0.1. The average river age was 3.6 years.

The average size of grilse was 52.8 cm and 3.4 lb (1.54 kg), and that of the sea-age class 2 was 75.3 cm and 10.6 lb (4.81 kg). Four per cent of the grilse and 28% of older salmon from Bay of Islands contained food; after July 22 no fish containing food was found. Capelin formed the predominant food item, and, almost always, the remainder was fish of other species.

A survey of the main Humber River and its tributaries revealed a number of natural obstructions to the passage of salmon. A brief description of these is given, together with some suggestions for improvement. Access of anadromous salmon to Grand Lake and tributaries has been cut off by a dam. The lake now contains lake salmon, brook trout, and Arctic char.

INTRODUCTION

The Humber River is one of the best salmon streams in Newfoundland. It supports a good commercial fishery, and its yield to anglers averaged highest of all Newfoundland rivers during the period 1942–1963 (average 1794 fish, range 222–5075). Its nearest rival was the Gander River, with an average of 1344 fish caught and range from 540 to 2682.

The Humber is situated on the west coast of Newfoundland (Fig. 1), emptying into Humber Arm of Bay of Islands. It is approximately 115 miles long (1 mile = 1.609 km) and has a total drainage area of 2955 square miles (1 mile^2 = 2.590 km^2). Of the rivers in Newfoundland it ranks third in length and second in drainage area. Humber Arm is 16 miles long and 2 miles wide with depths extending to 110 m. Bay of Islands proper is 11 miles long and 15 miles wide with the greatest recorded depth being 289 m (depths from Lauzier, 1957).

[1]Received for publication October 30, 1964.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

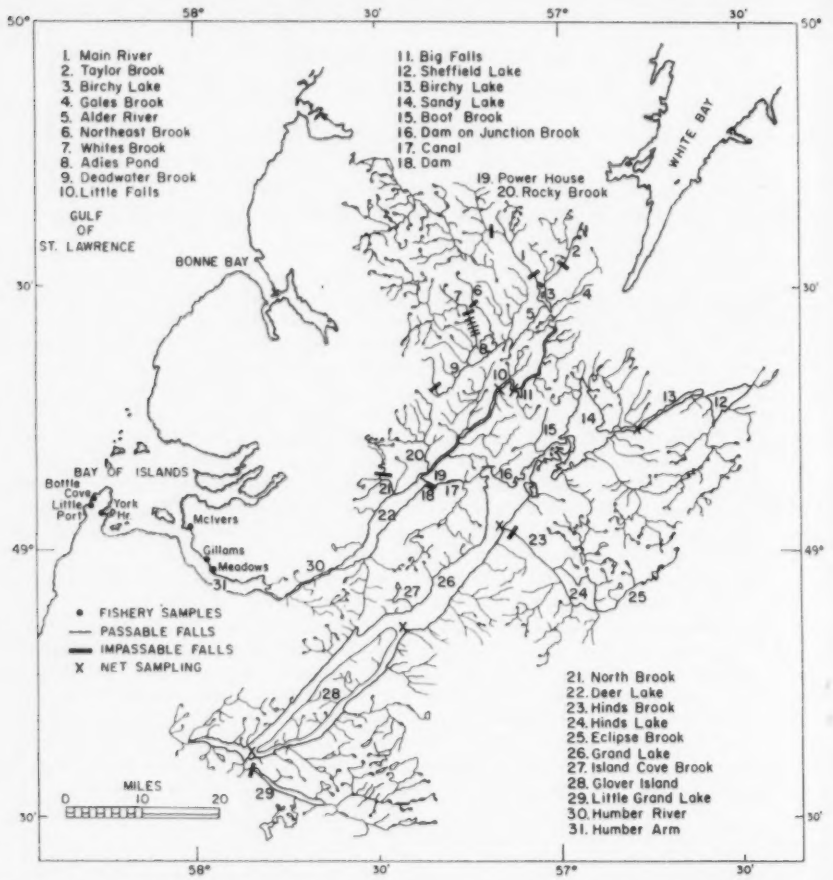


FIG. 1. Map of Humber River, Humber Arm, and Bay of Islands showing important falls on tributary streams and places where samples were obtained from the commercial salmon fishery.

The purpose of these investigations was to gather any information on the life of the salmon of Bay of Islands and Humber River and on their environment which might be pertinent to the management of the resource in this area. During the 1942 season the salmon net fishery was sampled, and some information from river-caught fish was obtained.

In 1942 also, a survey was made of Humber Arm waters for possible pollution (Vavasour and Blair, 1955). In 1943 the main Humber River and its tributaries were inspected for general conditions affecting the welfare of salmon. It had been thought that accumulations of bark from annual wood drives might be detrimental to salmon spawning, but it was soon found that natural barriers to upstream movement presented a more serious problem. Attention was therefore diverted to these in order to ascertain the feasibility of providing fishways.

METHODS AND DEFINITIONS

Sampling and Measurements

Sampling of the commercial salmon fishery was done at Meadows, Gillams, and McIvers on the north side of Humber Arm, at York Harbour on the south side of Bay of Islands, and at Bottle Cove and Little Port just outside the entrance to Bay of Islands. The data collected included scale samples, length and weight measurements, sex, and determination of stomach contents. Most of the sampling was done at McIvers where additional information was obtained on catch, fishing effort, weather, and water temperature. Sampling was carried out daily from June 3 to August 15, 1942, which included the whole fishing season except for approximately a week at the beginning and a couple of weeks at the end. The 955 fish in the sample were distributed as follows: McIvers 793 (83.0%), York Harbour 115 (12.0%), Meadows 27 (2.8%), Gillams 7 (0.7%), Little Port 7 (0.7%), and Bottle Cove 6 (0.6%).

The angling catch on the Humber River was sampled by the wardens when time from their regular duties permitted. Only 39 samples were obtained.

Lengths were measured to the nearest centimetre, from the anterior end of the snout to the posterior end of the middle ray of the caudal fin (= fork length). The measuring board was marked with centimetre and half-centimetre divisions; measurements falling exactly on the half-centimetre line were taken to the adjacent even number. A spring hand-balance was used to weigh the fish to the nearest quarter-pound (113 g).

Age Categories

Scales taken from immediately above the lateral line and just anterior to the adipose fin were examined. They were mounted in De Faure's fluid, omitting the cocaine (Guyer, 1947), and were examined using a projector. Age could be readily determined, and the boundary between freshwater growth and sea growth was clear.

Throughout this paper the term "sea-age" or simply "age" refers to whole years spent at sea, unless otherwise indicated. Salmon which are returning to fresh water after 1+ years spent at sea are called grilse and are in sea-age class 1. They are "maiden" fish, i.e. are returning to fresh water for the first time. Other maiden fish are of sea-age classes 2 or 3, very rarely more. Repeat spawners are classified according to the number of times they had spawned previously — once, twice, or three times — irrespective of their total sea-age. Kelts are salmon which spawned the previous autumn and are returning to sea. In Newfoundland the word "salmon" is often used in a restricted sense to mean fish of sea-age 2 or more, i.e. excluding grilse. This usage is adopted in parts of the text, but to avoid confusion in such cases the word is always written inside quotation marks ("salmon").

The term "river age" is the number of years spent in a river from the spring of hatching to the spring of the year during which seaward migration takes place. It was determined here by examination of the scales of adult

salmon, and actually refers to the number of winter-checks or annuli in the small central area of each scale which is formed during river life. River-age classes 2, 3, 4, 5, and 6 are represented in this material.

Stream Inspection

From July 29 to September 28, 1943, the main tributaries of the Humber were inspected. The method of travel was by canoe when possible and on foot when a canoe was impractical. Obstructions were mapped roughly, and potential spawning areas were assessed. The classification of bottom materials given by Davis (1938) was used: *sand*, microscopic to $\frac{1}{8}$ inch in diameter; *fine gravel*, $\frac{1}{8}$–$\frac{1}{2}$ inch; *coarse gravel*, $\frac{1}{2}$–3 inches; *rubble*, 3–12 inches; *small boulders*, 12–24 inches; and *large boulders*, over 24 inches.

THE COMMERCIAL FISHERY

Gear Used

Two types of gear are used primarily for salmon by commercial fishermen. Floating gill nets are of 5 or 6 inches stretched mesh (2.5 or 3 inches bar mesh). Salmon traps are of 5 inches stretched mesh (1 inch = 2.54 cm). Cod traps are also used in the area, and both grilse and older salmon are caught in these. The cod traps are 4 or 5 inches stretched mesh, and to some of these are attached salmon gill nets of 5- or 6-inch mesh, which thus form the leader of the cod trap.

Season of Run

According to the fishermen at McIvers, the time of the run of older salmon is usually from the last week of May to the first week of August, with the peak around June 15. Those taken in August are large fish averaging about 15 lb, but only a few are caught. The grilse run extends from June 15 to the last week in August, with the peak during the first week of July. Fishermen were fairly certain of the time of the run of older salmon, and the times given for the different sampling places were very similar. At most places, however, they were not definite in regard to the time of the grilse run. The reason is that most of the gill nets are of 6-inch mesh and therefore do not catch many grilse, but most grilse are caught in cod traps which are not placed in the water until the peak of the run of older salmon is past. Numbers of kelts were taken at the beginning of the salmon season and only an occasional one later, but they have been excluded from the samples. Most of the fish caught in gill nets were headed into the bay, which is to be expected if they are Humber River salmon.

Catch and Catch per Unit of Effort

No good records of total Bay of Islands and Humber Arm commercial catch are available for 1942, but I estimate it to be in the range 3000–4500

fish. Salmon catch records at McIvers were obtained for the 1942 season from 14 gill-net fishermen, of whom eight fished alone and six fished in pairs. Their catch, shown in Table I and Fig. 2, has been classified by size into the trade categories of grilse and "salmon," the point of division being at 6 lb. The total catch of these men for the season was 2191 fish, and the average daily catch was 22.8. The average amount of gear used per day was 3174 square fathoms of netting and the average catch per 1000 square fathoms per day was 7.2 fish; hence it required 139 square fathoms of netting to catch 1 fish in 1 day (1 fath^2 = 3.345 m^2).

These figures may be compared with those obtained from 10 fishermen prosecuting the fall salmon fishery in 1952 at Twillingate on the northeast coast of Newfoundland (Anon., 1954, p. 52). At Twillingate the average catch per 1000 square fathoms per day was half that at McIvers in terms of numbers, but by weight it was only slightly less because the fish were larger.

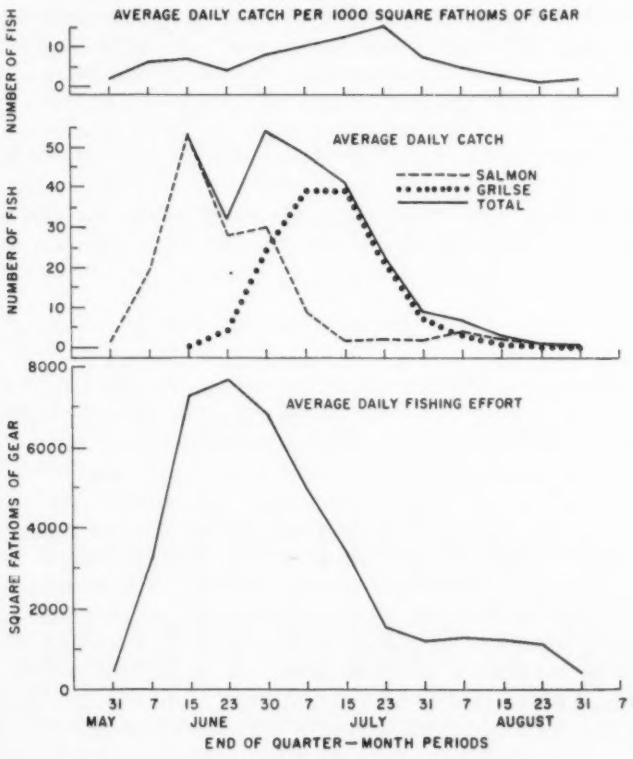


FIG. 2. Average daily fishing effort, average daily catch, and average daily catch per 1000 square fathoms of gear by quarter-month periods, for 14 fishermen fishing gill nets at McIvers, Bay of Islands, 1942 (data from Table I).

TABLE I. Total catches (in numbers) and daily averages, by quarter-month periods, for grilse and older "salmon" caught by 14 gill-net fishermen at McIvers, Bay of Islands, in 1942. Also shown is the amount of gear used, and the catch per unit of gear. Grilse and "salmon" were classified by size (1 square fathom = 3.345 square metres).

End of quarter-month period	Square fathoms of gear		Number of fish						Fish per 1000 square fathoms per day		
			Grilse		"Salmon"		Total				
	Total	Av.	No.	Av.	No.	Av.	No.	Av.	Grilse	"Salmon"	Total
May 31	3,600	450	0	...	7	0.9	7	0.9	...	1.9	1.9
June 7	21,388	3055	0	...	132	18.9	132	18.9	...	6.2	6.2
" 15	58,426	7303	3	0.4	421	52.6	424	53.0	0.1	7.2	7.3
" 23	61,526	7691	31	3.9	227	28.4	258	32.3	0.5	3.7	4.2
" 30	47,499	6786	166	23.7	209	29.9	375	53.6	3.5	4.4	7.9
July 7	34,469	4924	274	39.1	61	8.7	335	47.9	7.9	1.8	9.7
" 15	27,066	3383	311	38.9	14	1.8	325	40.6	11.5	0.5	12.0
" 23	12,328	1541	170	21.2	14	1.8	184	23.0	13.7	1.2	14.9
" 31	9,908	1238	56	7.0	13	1.6	69	8.6	5.7	1.3	7.0
Aug. 7	9,114	1302	19	2.7	27	3.9	46	6.6	2.1	3.0	5.1
" 15	9,296	1162	8	1.0	16	2.0	24	3.0	0.9	1.7	2.6
" 23	8,600	1075	3	0.4	6	0.8	9	1.1	0.3	0.7	1.0
" 31	1,500	375	2	0.5	1	0.2	3	0.8	1.4	0.6	2.0
Total:	304,720	3174	1043	10.9	1148	12.0	2191	22.8	3.4	3.8	7.2

Figure 2 shows two peaks in the total average daily catch, one during the quarter-month period ending June 15 and the other during the period ending June 30. The first peak corresponds with the peak of the run of "salmon," and the second peak reflects moderate numbers of the declining "salmon" run and the rising grilse run. The amount of net fished increased with the rise in the "salmon" run, reached a peak during the quarter-month period following the peak "salmon" catch, and thereafter decreased at about the same rate as the "salmon" run. During the best part of the grilse run the fishing effort was decreasing but the catch per unit of effort was increasing. It is obvious from Fig. 2 that the fishermen showed less interest in catching grilse than they did in catching "salmon." The fish trade prefers "salmon" to grilse because they are larger and more economical to handle, and they pay fishermen less per pound for grilse.

Ratio of Grilse to Older Salmon

Because fewer nets are fished during the grilse run, and because their mesh size is such as to take "salmon" more efficiently than grilse, the gross catch figures underestimate the relative importance of grilse in the total run (as it comes in from the sea). The seasonal average catch per unit of gear set might be a better index of relative abundance of the two types, but it is still biassed by the lesser vulnerability of the grilse to the nets in use. In 1942 the two indices were almost the same among the specially recorded catch of 14 gill-net fishermen at McIvers (Table I). Grilse were 48% of their total catch, while the mean catch per 1000 square fathoms of net for the season was 3.4 for grilse and 3.8 for "salmon," or 47% and 53%.

AGE COMPOSITION AND SIZE

Sea Age

The kinds of salmon represented among the 955 fish sampled from the Bay of Islands commercial catch were maiden fish of sea-age classes 1 (grilse), 2, and 3, and previously-spawned fish (Table II). The main sea-age classes for the entire season were grilse (57.2%) and 2-year maiden salmon (32.8%). Grilse were less numerous in June than sea-age class 2, but predominated during the rest of the season. Sea-age class 3 of maiden fish was not represented at all until August, whereas previously-spawned fish had a higher representation in the first half of June than later in the season.

The sea-age composition of the samples of the angling catch on the Humber River is given in Table III. The proportions of grilse and of previously-spawned salmon were much the same as in the commercial catch, but the sea-age class 3 salmon had a much higher representation than in the commercial catch. The Lower Humber (below Deer Lake) is noted for catches of large salmon, and all the sea-age class 3 salmon in the samples were taken at Steady Brook on the Lower Humber. In the samples from the Lower Humber 10 out of 12 fish were over 12 lb in weight, whereas on the Upper Humber only 2 out of 27 fish were over 12 lb.

TABLE II. Percentage of the various sea-age classes in samples from the commercial salmon fishery of Bay of Islands.

	Maiden fish — years at sea			Previously spawned				Total older than grilse	No. of fish
	Grilse	2 +	3 +	Once	Twice	Three times	Total		
	%	%	%	%	%	%	%	%	
June 1–15	2.6	76.8	...	18.1	2.5	...	20.6	97.4	155
" 16–30	39.6	50.6	...	9.4	0.4	...	9.8	60.4	255
July 1–15	81.1	14.0	...	3.4	0.9	0.6	4.9	18.9	349
" 16–31	83.0	8.2	...	7.0	1.8	...	8.8	17.0	171
Aug. 1–15	64.0	8.0	20.0	8.0	...	...	8.0	36.0	25
Total:	57.2	32.8	0.5	8.2	1.2	0.2	9.5	42.8	955

TABLE III. Percentage of the various sea-age classes in samples from the angling catch on the Humber River in 1942.

	Maiden fish — years at sea			Previously spawned				Total older than grilse	No. of fish
	Grilse	2 +	3 +	Once	Twice	Four times	Total		
	%	%	%	%	%	%	%	%	
June 16–30	70.6	23.5	...	5.9	...	...	5.9	29.4	17
July 1–15	100.0	...	...	...	...	...	...	...	2
" 16–31	66.7	...	...	...	...	33.3	33.3	33.3	3
Aug. 1–15	...	33.3	66.7	...	...	...	...	100.0	3
" 16–31	44.4	...	33.3	11.1	11.1	...	22.2	55.6	9
Sept. 1–15	...	...	100.0	...	...	...	...	100.0	2
" 16–30	66.7	...	33.3	...	...	...	...	33.3	3
Total:	56.4	12.8	20.5	5.1	2.6	2.6	10.3	43.6	39

In angling statistics collected by the Department of Fisheries of Canada salmon are divided into two classes: those under 6 lb are called grilse, while those 6 lb and over are "salmon." For the years 1954 to 1963 the percentage of "salmon" ranged from 35 to 95% on the Lower Humber but only from 3 to 8% on the Upper Humber. For the whole river the range is 4–14%.

River Age

River-age classes 3 and 4 contained 42% and 52%, respectively, of the fish examined from Bay of Islands, or 94% in all (Table IV). River-age classes 2, 5, and 6 were poorly represented. The average river age was 3.6 years for grilse and 3.5 for sea-age class 2; the grand average was 3.6 years.

In the sample of 34 fish from the Humber River, river-age classes represented were 3, 4, and 5 (Table V), the average being 3.9 years.

Table IV. Percentage of the various river-age classes, and average river age, for different sea-age classes in Bay of Islands samples (PS1 = previously spawned once).

Sea-age class	River-age class					No. of fish	Average river age
	2	3	4	5	6		
	%	%	%	%	%		*years*
1	2.3	40.4	52.3	4.7	0.2	512	3.6
2	1.7	50.0	46.6	1.7	...	290	3.5
PS1	1.4	29.2	61.1	8.3	...	72	3.8
All other	5.9	11.8	76.5	5.9	...	17	3.5
Total:	2.1	42.1	51.6	4.0	0.1	891	3.6

Table V. Percentage of the various river-age classes, and average river age, for different sea-age classes in Humber River samples.

Sea-age class	River-age class			No. of fish	Average river age
	3	4	5		
	%	%	%		*years*
1	25.0	70.0	5.0	20	3.8
2	...	100.0	...	4	4.0
3	14.3	71.4	14.3	7	4.0
PS1	...	100.0	...	2	4.0
All other	100.0	...	...	1	3.0
Total:	20.6	73.5	5.9	34	3.9

"Lake-Type" Growth

So-called "lake-type" freshwater growth was identified on the scales of some salmon on the east coast of Newfoundland and Labrador in 1939 (Blair, 1943); though it is not certain whether this actually represents growth in a lake or whether it is merely rapid river growth. The same type of growth was found among salmon from the Bay of Islands and Humber River (Table VI). With one exception the "lake" growth was preceded by 1–4 years of "river" growth; the exception exhibited "lake" growth only (3 years) in fresh water. The percentage of the total sample showing "lake" growth was 14% in Bay of Islands, 12% in the Humber River, and 13% on the east coast of Newfoundland and Labrador. In all three areas the grilse included a higher proportion of fish showing "lake" growth than did sea-age class 2. Good freshwater growth means larger than average smolt size for any river-age class, and larger smolts tend to return sooner from the sea than smolts of smaller size.

Length and Weight

The size of the salmon in the Bay of Islands catch increased considerably with each additional year of sea life (Table VII). The average size of grilse was 52.8 cm and 3.4 lb. This was considerably smaller than for the east coast of Newfoundland and Labrador, where the average size in 1939 was 54.5 cm and 4.6 lb (Blair, 1943). Bay of Islands grilse were in fact smaller than those on any individual section of the east coast: the two sections having the smallest grilse were Conception Bay (54.2 cm, 3.9 lb) and Trinity Bay (53.5 cm, 4.1 lb). The difference between these two bays and the Bay of Islands samples is apparently representative of the respective stocks, since the types of gear used are the same in all three bays.

The average weight of sea-age class 2 in the Bay of Islands was about the same as the average for the east coast of Newfoundland and Labrador, but the average length was about 2 cm longer (Table VII). In weight the salmon in this class were similar to salmon from Bonavista Bay to the Strait of Belle Isle, but were heavier than those south of this area. In length they exceeded those from all sections of the Labrador and Newfoundland coasts south of Hamilton Inlet (Blair, 1943).

Among the 39 salmon sampled from the Humber River, the grilse were about the same size as those in the Bay of Islands samples, but sea-ages 2 and 3, and the previously spawned salmon, were all larger. This may have been due to selective sampling of larger fish from the anglers' catches, or to greater attention being given to the Lower Humber River by anglers seeking trophy fish.

Food and Nutrition

Stomach Contents

Of the 919 stomachs examined from the Bay of Islands, only 127 (14%) contained food (Table VIII). The number of fish with food in their stomachs

TABLE VI. Percentage of fish with "lake-type" of scale growth in each sea-age class for Bay of Islands, Humber River, and the east coast of Newfoundland and Labrador. The total number of fish in each sea-age class is given in parentheses.

	Maiden fish — years at sea			Previously spawned					
Area	Grilse	2 +	3 +	Once	Twice	Three times	Total	Total older than grilse	Total
Bay of Islands	16.2(512)	11.0(290)	0.0(5)	5.6(72)	20.0(10)	0.0(2)	7.1(84)	10.0(379)	13.6(891)
Humber River	15.0(20)	0.0(4)	0.0(7)	0.0(2)	100.0(1)	...	33.3(3)	7.1(14)	11.8(34)
East coast	28.7(710)	6.0(1435)	0.0(47)	7.5(279)	20.0(5)	...	7.7(284)	6.1(1766)	12.6(2476)

TABLE VII. Average length and weight of salmon in each sea-age class in Bay of Islands in 1942.

Sea-age class	Length	Weight	Weight	No. of fish
	cm	*lb*	*kg*	
1	52.8	3.4	1.54	538
2	75.3	10.6	4.81	309
3	88.8	18.9	8.57	5
Previously spawned	73.8	9.9	4.49	91

decreased rapidly from 45% during the first half of June to none in August. No fish were found with food in their stomachs after the third week in July. Belding (1935) also observed a marked decline in the number of salmon feeding in salt water after the middle of June, and none of his fish taken after July 20 contained food.

The Bay of Islands grilse were not feeding as much as the older salmon; only 4% of the grilse had food in their stomachs, as compared with 28% of the "salmon." The same was true during each half-monthly period of the season, except for the first half of June when only four grilse were sampled (Table VIII).

The types of food found in the 127 stomachs containing food are given in Table IX. Capelin was the dominant food item for these almost exclusively piscivorous fish. This being so, it is possible that the number of salmon containing food is related to the quantity and movements of capelin. Templeman (1948) showed that capelin occurred in the Bay of Islands area in 1942, during the period June 15–22, and gives the spawning season as June 19–22. Apparently the main body of older salmon and the capelin moved into Bay of Islands at about the same time (Fig. 2), but the capelin arrived earlier than the grilse and moved out again before the main body of grilse arrived. For the period June 16–30, which includes the time when capelin were reported in Bay of Islands, 25% of the older salmon and 12% of the grilse contained food.

SCALE ABSORPTION

Absorption of the margins of the scales is a feature of the spawning migration of salmon; the incidence of scale absorption may be related to feeding and state of nutrition. Among the 955 grilse and older salmon sampled from the Bay of Islands commercial fishery from June 3 to August 15 there was only one fish on which scale absorption had started. This fish, a grilse, was taken July 20 and did not have any food in its stomach.

Of the 39 grilse and older sea-year salmon from Humber River from June 18 to September 24 there were 16 fish (41%) with scale absorption. These

TABLE VIII. Percentage of grilse and older "salmon" with food in their stomachs during various periods of the run in Bay of Islands in 1942.

Period	Grilse		"Salmon"		Total	
	%	*No.*	%	*No.*	%	*No.*
June 1–15	50.0	4	45.0	140	45.1	144
" 16–30	12.1	99	25.0	148	19.8	247
July 1–15	2.2	275	8.1	62	3.3	337
" 16–31	0.7	142	3.4	29	1.2	171
Aug. 1–15	0.0	16	0.0	9	0.0	25
Total:	3.9	536	27.7	383	13.8	919

TABLE IX. Types of food found in 127 stomachs of grilse and older salmon in Bay of Islands in 1942. The left-hand panel shows the number and percentage of stomachs that contained each combination of food items indicated. The right-hand panel shows the number and percentage of stomachs that contained each item listed.

Type of food	Stomachs	
	No.	%
Capelin	100	78.7
Lance	9	7.1
Capelin and lance	8	6.3
Shrimp	2	1.6
Capelin and shrimp	1	0.8
Capelin and cod	1	0.8
Capelin and smelt	1	0.8
Cod	1	0.8
Herring	1	0.8
Brook trout	1	0.8
Unidentified	2	1.6
Total:	127	100

Type of food	Occurrences	
	No.	%
Capelin (*Mallotus villosus*)	111	87.4
Lance (*Ammodytes americanus*)	17	13.4
Shrimp	3	2.4
Cod (*Gadus morhua*)	2	1.6
Smelt (*Osmerus mordax*)	1	0.8
Herring (*Clupea harengus*)	1	0.8
Brook trout (*Salvelinus fontinalis*)	1	0.8
Unidentified	2	1.6

fish were taken between August 9 and September 24 and none contained any food in their stomachs.

SEX

The sex of 919 fish from Bay of Islands and 32 fish from Humber River was determined by inspection of the gonads (Table X). The overall proportion of females in the two samples was almost identical. At all seasons males predominated among the grilse (average 63%), while females predominated among the older maiden fish (94%). Repeat spawners exhibited a moderate excess of males early in the season, and an excess of females later.

RIVER SURVEYS

Main Humber River

From the mouth of Humber River to Deer Lake, a distance of approximately 15 miles, the river is wide and deep with no obstructions (1 mile = 1.609 km). Deer Lake is 16 miles long and has an area of 24 square miles (62 km^2); there are a few small tributaries flowing into it. The main river below Deer Lake is generally referred to as the Lower Humber and that above Deer Lake as the Upper Humber.

The river above Deer Lake was travelled many times by canoe. Despite extensive logging operations no evidence was found of accumulations of bark which might be deleterious to spawning success.

There are two falls on the Upper Humber, Little Falls and Big Falls. Little Falls is about 18 miles above Deer Lake and consists of a few rapids. The greatest drop at the foot of the rapids would be about 3 ft and at a slope of 45°. Big Falls is about 23 miles above Deer Lake (Fig. 3). The highest part of the fall is in the middle where it is about 10 ft high; the lowest place on the left side is about 5 ft high and on the right side 4 ft high. At the time of the 1942 survey, the strong flow of water made it difficult for salmon to get over this fall and it was reported that salmon were sometimes killed by jumping through the down-pouring water and striking the rock behind. The pool below the fall, where the salmon lie, is about 400 yards long (360 m). Since this survey, a trench has been excavated near the left bank by the Department of Fisheries of Canada (Fig. 3).

North Brook

This is a small brook on the north side of Deer Lake. About 5 miles up from the mouth it has four impassable falls in a 148-ft stretch of the stream. The falls range in height from 8 to 16 ft.

Rocky Brook

This stream flows into the Upper Humber 1 mile upstream from the head of Deer Lake. It has no obstructions at the present time. A dam was built at the mouth of the East Branch of Rocky Brook in 1927 but it has since rotted out and is not now an obstruction.

TABLE X. Percentage of the sexes in each sea-age class in the Bay of Islands samples in 1942.

	Maiden fish									Previously spawned			Total		
	Grilse			2 +			3 +								
	M	F	Total	M	F	Total	M	F	Total	M	F	Total	M	F	Total
	%	%	*No.*	%	%	*No.*	%	%	*No.*	%	%	*No.*	%	%	*No.*
June 1–15	75.0	25.0	4	2.7	97.3	110	...	...	...	60.0	40.0	30	16.7	83.3	144
" 16–30	60.6	39.4	99	6.4	93.6	125	...	...	...	65.2	34.8	23	33.6	66.4	247
July 1–15	64.0	36.0	272	6.7	93.3	45	...	...	...	37.5	62.5	16	55.0	45.0	333
" 16–31	61.0	39.0	141	14.3	85.7	14	...	...	...	40.0	60.0	15	55.3	44.7	170
Aug. 1–15	75.0	25.0	16	0.0	100.0	2	40.0	60.0	5	50.0	50.0	2	60.0	40.0	25
Total:	63.0	37.0	532	5.4	94.6	296	40.0	60.0	5	53.5	46.5	86	43.4	56.6	919

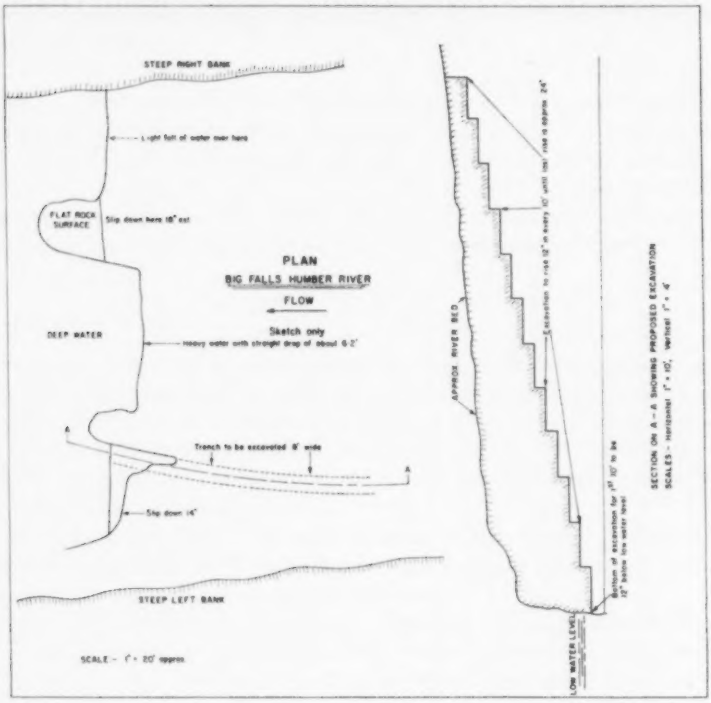


FIG. 3. Elevation and plan of improvements made to Big Falls, upper Humber River. Courtesy of the Department of Fisheries of Canada.

JUNCTION BROOK

This brook, which is 6 miles above Deer Lake, was formerly the sole outlet of Grand Lake. It now has an impassable power dam on it, which diverts the waters of Grand Lake to a power station at Deer Lake by way of a canal (Fig. 1). The dam on Junction Brook is not provided with a fishway, and sea-going salmon are thereby deprived of the use of a drainage area of 1850 square miles (Anon., 1960) including several lakes whose areas (square miles) are as follows: Grand 140, Sandy 43, Hinds 14, Sheffield 9, Birchy 4.3, and Little Grand 4.3 (1 mile^2 = 2.59 km^2). Salmon can move freely from Grand Lake to Sandy, Birchy, and Sheffield Lakes, but there is an impassable fall at the outlet of Little Grand Lake and one on Hinds Brook about $\frac{1}{2}$ mile from the mouth.

The spillway of the dam at the Deer Lake end of the diversion canal is about 20 ft high on a slope of 45°, and a short distance below this there is another drop of about 5 ft.

Gales Brook

This enters Humber River about 38 miles above Deer Lake. It was travelled almost to its source and no obstructions were seen, but the brook was not followed at all times. The bottom is mud for about 1 mile from the mouth and the remainder consists of a mixture from sand to boulders. In some places the bottom is mainly rubble, small boulders, and large boulders but in other places it is mainly sand to coarse gravel. Very little bedrock was seen.

Deadwater Brook

This is a small brook, 13 miles long, which flows into the upper end o Adies Pond. About 8 miles from the mouth of Deadwater Brook there is an impassable fall consisting of two vertical drops of about 50 ft in all. For the first half-mile from the mouth the bottom consists of mud plus bits of bark and above this a mixture of sand to small boulders with some bedrock. Salmon spawn in all the gravelly places along this brook. The driving of pulpwood has widened this brook considerably.

Whites Brook

This is 25 miles long and flows into Adies Pond on the north side. Three and a half miles from the mouth there is an impassable fall with a 13-ft vertical drop. The main flow is on the left side and there is enough space on the right side to make a fishway. Between this fall and the mouth there are several small passable falls ranging in height from 3 to 7 ft. Also, from one-half to three-quarters of a mile above this fall there are several low passable falls some of which could be improved by blasting to make the pools deeper.

At the mouth of the brook there is a mixture of sand, gravel, and small boulders with scattered large boulders. Farther up, the bottom consists mainly of stones the size of rubble and larger. Salmon spawn mainly in a half-mile stretch beginning near the mouth according to the Fishery Officer, and he believes they stay in the pond by day and enter the brook at night.

Northeast Brook

This is 14 miles long and flows into the northeastern end of Adies Pond. It has an impassable fall about 4 miles from the mouth which consists of several drops. There is also a flood channel but it is steeper than the fall. A fishway in the fall itself seems practical; a possible design is shown in Fig. 4. About 600 ft above this fall there are two 4-ft falls separated by 100 ft of rapids.

Right at the mouth the bottom is mud, sand, fine gravel, and coarse gravel. Sand, fine gravel, and coarse gravel or a mixture of these are also found from the mouth to about 3 miles upstream but the bottom is mainly coarse gravel. From there to the fall the bottom materials are small and large boulders which are not good for spawning.

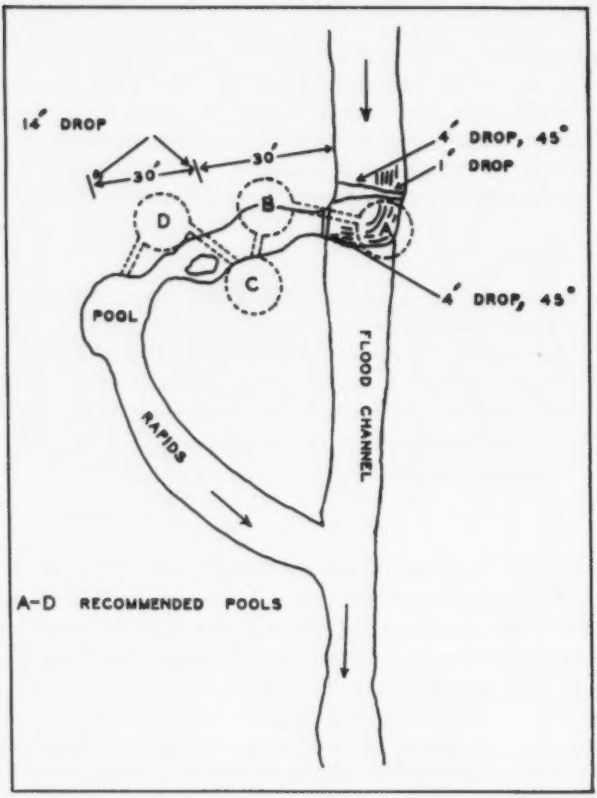


FIG. 4. Rough plan of the fall on Northeast Brook, 4 miles from the mouth. Distances are in feet.

TAYLOR BROOK

This brook is 14 miles long and is a tributary of Birchy Lake, an expansion of Main River (Fig. 1). Three and a half miles from the mouth of Taylor Brook there is an impassable fall which is a vertical drop of 8 ft (Fig. 5). Lack of a deep pool at the foot of the fall would make it difficult for salmon to get over it. Recommended improvements include deepening of this pool and taking 2 ft off the crest of the fall. About 15 ft below this fall there is another 8-ft drop but this is on a slope. It is difficult to say whether salmon would be able to get over this drop or not but it could be improved by widening to reduce the strength of the current. A short distance below this fall there are four low passable falls.

From the mouth to the falls the bottom consists of mud, sand, fine gravel, coarse gravel, rubble, or various mixtures of these. A few small and large boulders are found at the upper end of this section of the brook. There is no

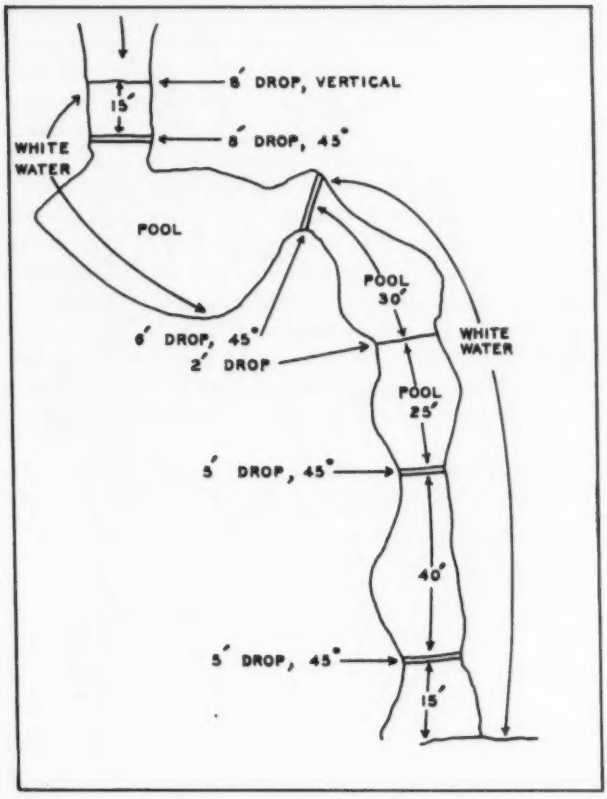


FIG. 5. Rough plan of falls on Taylor Brook, 3½ miles from the mouth. Distances are in feet.

rubble near the mouth and in general the bottom material becomes coarser going upstream. Coarse gravel is the commonest material and the entire section from the mouth to the falls is suitable for salmon spawning.

MAIN RIVER

This stream is 42 miles long, its drainage area being next in size to the Grand Lake watershed. Its lower reaches include Birchy Lake (not to be confused with the larger Birchy Lake in the Grand Lake drainage). It joins with Alder River to form the Upper Humber River (Fig. 1). Five miles from the mouth of the river and half a mile above Birchy Lake there is an impassable, vertical fall which is 13 ft high (Fig. 6). Water flows over an overhanging shelf at the top of the fall at such speed that it descends at an angle of 45° to the vertical and at the foot of the fall strikes a ledge which would make it difficult for salmon to jump any great height. To the right of the fall there

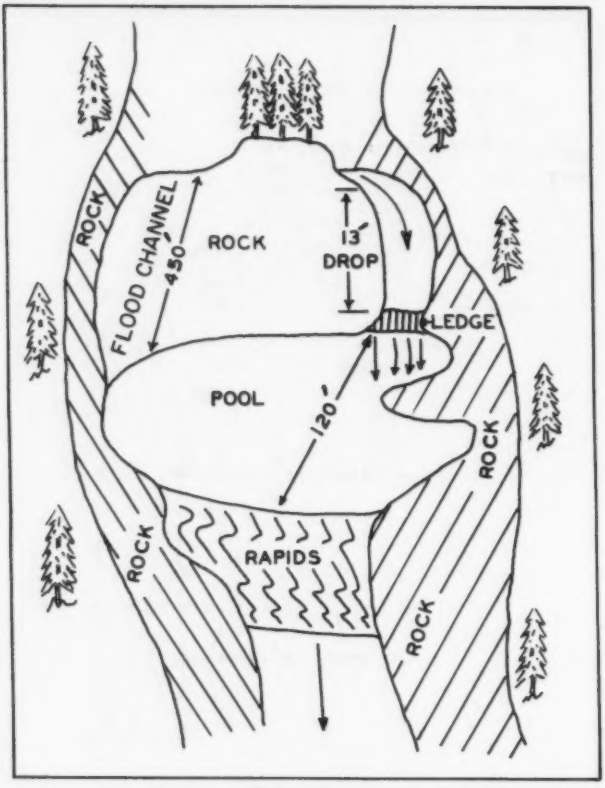


FIG. 6. Rough plan (not to scale) of the fall on the Main River, 5 miles from the mouth. Distances are in feet.

is a flood channel which is 450 ft long where a fishway could be made at very little expense. According to the Fishery Officer there are three or four small falls 8.5 miles above this one which he considers impassable.

In the half-mile from the upper end of Birchy Lake to the impassable fall the river bottom is composed of a mixture of sand, gravel, and boulders, but sand is not very plentiful. With increasing distance upstream gravel gets scarcer and larger stones are more plentiful.

GRAND LAKE, SANDY LAKE, BIRCHY LAKE

Anadromous salmon were present in Grand Lake, and presumably in its accessible tributaries, up to the time of the construction of the dam on Junction Creek. The caretaker at the powerhouse reported that when the station was first operated large quantities of kelts were hauled out of the forebay and thrown over the bank. Also, during the first 3 or 4 years that the system was in operation, young salmon 10–12 inches long were plentiful in the forebay.

Lake salmon (ounaniche) now occur in the Grand Lake system, and of course may have occurred there prior to construction of the Junction Creek dam. In 1943 a Mr Vardy of Howley reported salmon of 3–4 lb taken each year at the mouth of Hinds Lake.

From September 12 to 17, 1943, an unsuccessful effort was made to catch salmon in nets of $4\frac{1}{4}$- and 5-inch stretched mesh which were 72 ft long and 12 ft deep. The net was set overnight at four widely scattered places, as follows: A — Grand Lake, south side, opposite the upper end of Glover Island; B — the same, opposite the lower end of Glover Island; C — the same, at the mouth of Hinds Brook; D — at the mouth of Birchy Lake (Fig. 1). The catch consisted of brook trout (*Salvelinus fontinalis*) only, and the best catch was obtained at the mouth of Birchy Lake (Table XI). The net was set on the surface and out from the shore. The trout were meshed from the surface down to 9 ft. In Grand Lake most of them were meshed near the shore end of the net but at the mouth of Birchy Lake most were meshed in the middle of the

TABLE XI. Catch data for brook trout netted in Grand and Birchy Lakes in 1943, using 24 square fathoms (80 m²) of gill net in each set. See the text for location of stations A–D.

Date	Station	Catch	Fishing time	Catch per hour
		fish	*hr*	*fish/hr*
Sept. 12–13	A	4	19.2	0.21
" 13–14	B	1	14.5	0.07
" 14–15	C	18	16.5	1.09
" 16–17	D	68	14.7	4.63

TABLE XII. Length, weight, and sex of brook trout netted in Grand and Birchy Lakes in 1943. See the text for the location of stations A–D (1 lb = 545 g).

	Length (*cm*)				Weight (*lb*)				Sex (%)		
Station	Av.	Max.	Min.	No.	Av.	Max.	Min.	No.	M	F	No.
A	42.4	46.0	39.0	5	2.1	2.75	1.75	5	80.0	20.0	5
B	38.0	38.0	38.0	1	...	...	...	...	...	...	...
C	40.1	43.0	36.0	18	1.9	2.25	1.50	13	76.9	23.1	13
D	40.8	47.0	35.0	68	2.1	2.75	1.25	39	65.8	34.2	39
Total:	40.7	47.0	35.0	92	2.1	2.75	1.25	57	69.6	30.4	57

net. Of the 92 brook trout caught (91 in 4¼-inch mesh net, 1 in 5-inch mesh net) 35 were measured and released alive, and 57 were measured, weighed, and sexed. They averaged 40.7 cm long and 2.1 lb in weight (Table XII). Male trout were more numerous than female, the percentage of males being 69.6.

In 1949 Dr A. O. Blackhurst conducted some experimental netting in Grand Lake and caught mainly brook trout. However, he also caught a few Arctic char (*Salvelinus alpinus*) which were identified by Dr W. B. Scott of the Royal Ontario Museum, Toronto. The Arctic char were caught in deep water (36–80 fathoms).

ACKNOWLEDGMENTS

It is a pleasure to acknowledge the help received from the following officials of the Protection Service: Forest Inspector E. L. Stratton, Game Warden Jack Marshall, and especially Fishery Officer G. R. Nichols whose knowledge of the river was invaluable. The Newfoundland Department of Mines, Agriculture and Resources very kindly supplied the information on the size of lakes and the Humber River drainage. The Bowater's Newfoundland Pulp and Paper Mills, Ltd., assisted greatly by allowing us frequent use of their speedier transportation service on the Upper Humber.

Sampling of the fishery in Bay of Islands was done by Messrs Peter Loder and George Huxter, and Mr John Elford helped in fishing operations on Grand and Birchy Lakes. Assistance in preparing the paper was provided by Messrs A. P. Cowan, H. R. Mullett, and mainly F. A. Day.

REFERENCES

ANON. 1954. Newfoundland Fisheries Research Station, pp. 47–63. In *Ann. Rept. Fish. Res. Bd. Canada* for 1953.

ANON. 1960. Surface water supply of Canada; Atlantic drainage; southeastern Quebec, New Brunswick, Nova Scotia, Prince Edward Island and Newfoundland; climatic years 1956–57 and 1957–58. *Canada Department of Northern Affairs and National Resources, Water Resources Branch, Water Resources Paper* No. 123, 160 pp.

BELDING, DAVID L. 1935. The cause of the high mortality in the Atlantic salmon after spawning. *Trans. Am. Fish. Soc.* for 1934, **64**: 219–224.

BLAIR, A. A. 1943. Atlantic salmon of the east coast of Newfoundland and Labrador, 1939. *Newfoundland Dept. Nat. Res., Fish. Res. Bull.*, No. 13, 21 pp.

DAVIS, H. S. 1938. Instructions for conducting stream and lake surveys. *U. S. Bur. Fish., Fish. Circular*, No. 26, 55 pp.

GUYER, MICHAEL F. 1947. Animal micrology. Univ. Chicago Press, Chicago. 4th revised ed., 331 pp.

LAUZIER, L. 1957. Hydrographic features of the waters of the Bay of Islands, Newfoundland, in the autumn. *Bull. Fish. Res. Bd. Canada*, No. 111, pp. 287–317.

TEMPLEMAN, WILFRED. 1948. The life history of the caplin (*Mallotus villosus* O. F. Müller) in Newfoundland waters. *Newfoundland Dept. Nat. Res., Fish. Res. Bull.*, No. 17, 151 pp.

VAVASOUR, G. R., AND A. A. BLAIR. 1955. Pollution survey of Humber Arm and Exploits River. *J. Fish. Res. Bd. Canada*, **12**(5): 682–697.

NOTES

Seasonal Distribution of Monkfish Along the Canadian Atlantic Mainland

Monkfish (*Lophius americanus* Cuvier and Valenciennes) (Fig. 1) are among the many fish species caught by line and otter trawl which are not commercially exploited along the Atlantic coast of Canada.

Monkfish are found on the fishing banks of the western Atlantic from Newfoundland and the Gulf of St. Lawrence southward to North Carolina and in deep water as far south as Brazil (Connolly, 1920). In the eastern Atlantic, they occur from the Faroe Islands southward to the Cape of Good Hope (Bigelow and Schroeder, 1953).

Observations on the seasonal distribution of monkfish along the Canadian mainland were made during research surveys carried out by this Station since 1957 (Jean, 1964). These observations were made incidentally to those on commercially more important species, such as cod and haddock, which were

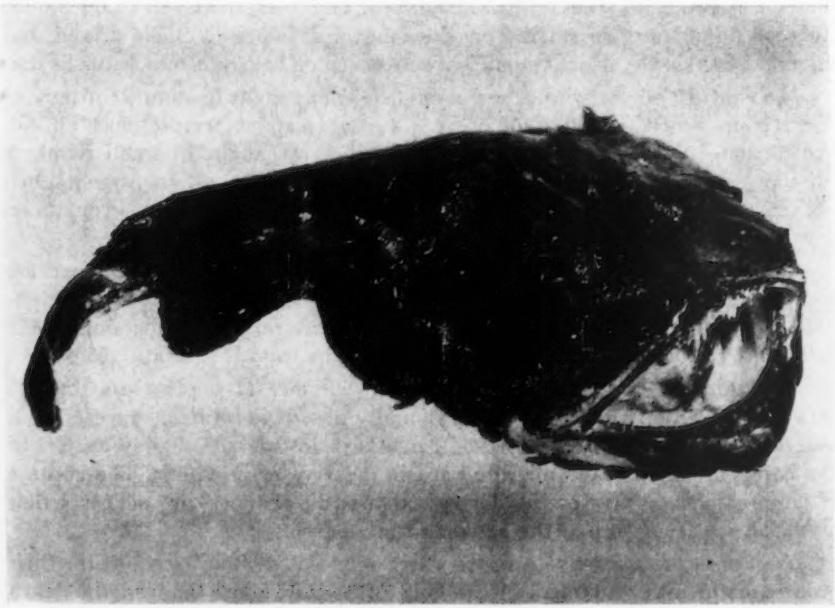


FIG. 1. Monkfish (*Lophius americanus* Cuvier and Valenciennes). Photo by P. M. Powles.

J. FISH. RES. BD. CANADA, **22**(2), 1965.
Printed in Canada.

the main objects of studies during these surveys (Jean, 1964; McCracken, 1964). This paper is based on the results of surveys up to and including April 1963. Summer surveys started in 1957 and covered the months from May to October. Winter surveys started in 1959 and extended from January to April. The areas explored extended from Gaspé southward to the northern edge of Georges Bank (Fig. 2), but did not include the waters off Newfoundland.

The characteristics of gear and research vessels, and the methods of survey were described by Jean (1964). The summer surveys were conducted mainly from the 67-ft *J. J. Cowie* (1957–58) and the 84-ft *Harengus* (1959–62). The winter surveys were carried out by the 177-ft *A.T. Cameron*.

The locations of all tows made during winter and summer surveys are shown in Fig. 2. Tows which did not catch monkfish are represented by small open circles. Those that caught monkfish are shown as black circles. The size of the circle is proportional to the average number of monkfish caught per tow, as shown in the symbol key (Fig. 2).

In winter, monkfish were scarce in the Gulf of St. Lawrence and off the Cape Breton coast. The few that were caught came from deep water along the western edge of the Laurentian Channel. Very few monkfish were caught on top of the Nova Scotia Banks in winter. At that season monkfish were found in deep water along the slopes and in the channels of the Scotian Shelf. The greatest numbers (up to 120 fish per $\frac{1}{2}$-hr tow) were caught on the seaward edges of Banquereau (the Gully), Sable Island, and Western and Emerald Banks. Smaller numbers were caught on the landward slopes of Sable Island and Emerald Banks. Occasional monkfish were taken off southwestern Nova Scotia.

In contrast to the winter, few monkfish were caught in summer in any of the regions fished. In the Gulf of St. Lawrence catches were almost nil. On the offshore Nova Scotia grounds, monkfish were caught in small numbers on top of the banks and only occasionally along the slopes. In August 1962, the northern edge of Georges Bank gave the best catches, but, even there, less than 10 monkfish per tow were caught.

The depths at which monkfish are caught in winter and summer are compared in Fig. 3. In winter, they are concentrated at 100–140 fath (180–255 m). In summer, they are more or less evenly distributed from about 15–120 fath (25–220 m), but are slightly more abundant from 15–50 fath (25–92 m).

The fact that monkfish are present in summer at depths less than 50 fath (92 m), from which they were virtually absent in winter, suggests that, like many other species (Jean, 1964), monkfish invade the shallow waters of the banks in summer and migrate back in deep water in winter. The absence of large catches at any of the depths explored in summer also suggests that monkfish scatter on top of the banks in summer.

Monkfish are a relatively warm-water species. This may account for their occurrence in fewer numbers in the Gulf of St. Lawrence than on the Nova Scotia Banks. Where present, however, monkfish are caught over a wide range of temperature both in winter and in summer. They are taken from

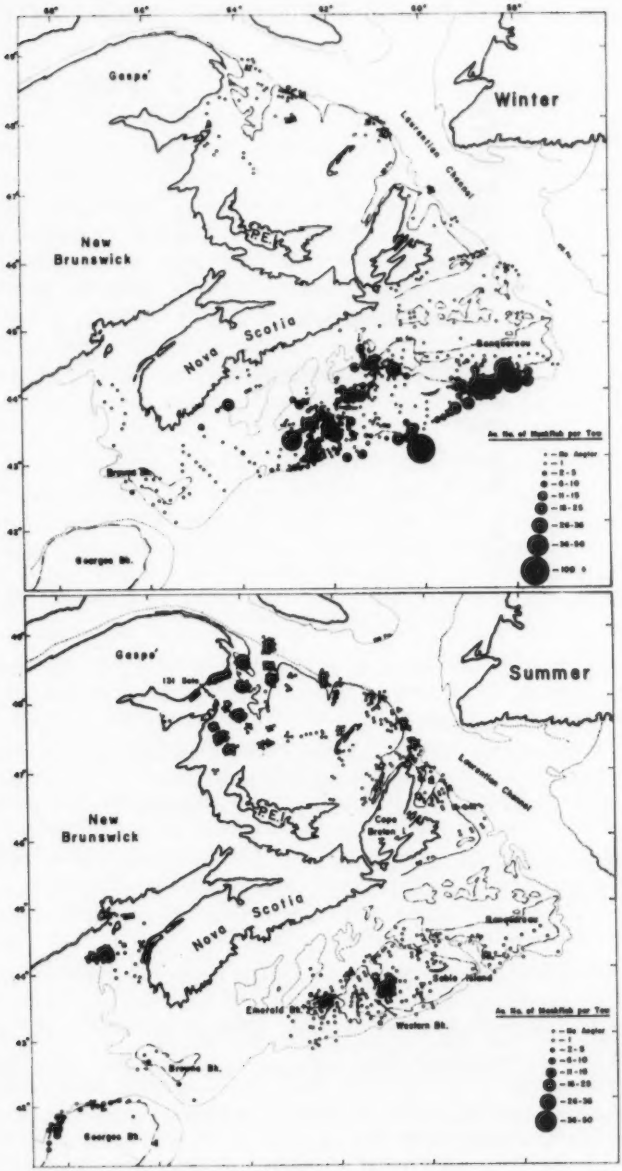


FIG. 2. Distribution of monkfish catches in research surveys along the Canadian mainland in winter and summer.

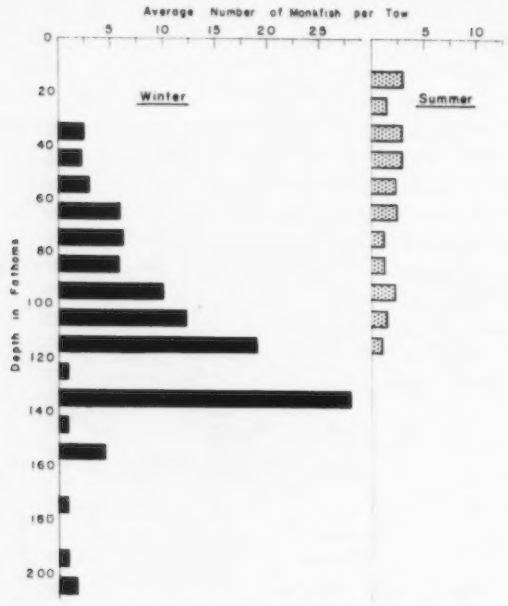


FIG. 3. Winter and summer distribution by depths of monkfish catches in research surveys.

32–48°F (0–10°C) in winter and from 32–54°F (0–12°C) in summer. The largest concentrations occur at about 37–42°F (3–6°C) in winter and about 41–48°F (5–9°C) in summer.

These observations suggest that monkfish, although not abundant enough to be fished alone on a commercial basis, could become an important addition to the catch of other species on the Nova Scotia Banks in winter.

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

YVES JEAN[1]

Received for publication June 1, 1964.

REFERENCES

BIGELOW, H. B., AND W. C. SCHROEDER. 1953. Fishes of the Gulf of Maine. *U. S. Fish and Wildlife Serv., Fish. Bull.*, 53, 577 pp. (Fish. Bull. No. 74.)

CONNOLLY, C. J. 1920. Histories of new food fishes. III. The angler. *Bull. Biol. Bd. Canada*, No. 3, 17 pp.

JEAN, Y. 1964. Seasonal distribution of cod (*Gadus morhua* L.) along the Canadian Atlantic coast in relation to water temperature. *J. Fish. Res. Bd. Canada*, **21**(3): 429–460.

MCCRACKEN, F. D. 1964. Distribution of haddock off the eastern Canadian mainland in relation to season, depth, and bottom temperature. Int. Comm. NW Atlantic Fish., Environmental Symposium, Rome, 1964. Contr. No. A-8.

[1]Present address: Fisheries Division, Dept. of Industry and Commerce, Quebec, P. Q.

Canadian Atlantic Salmon Recaptured Near Greenland

Since 1956 there have been reports of seven tagged European (Menzies and Shearer, 1957; Swain *et al.*, 1962; Carlin, 1962; Swain, 1963; Allan and Bulleid, 1963; Carlin, personal communication) and three North American (Kerswill and Keenleyside, 1961; Anon., 1962; Cutting, 1964) Atlantic salmon having been caught near west Greenland. Thus some salmon from Europe and North America come to a common area in the western Atlantic. Nielsen (1961) and Munch-Ellingsen (personal communication) imply that these are feeding salmon. Menzies (1949) suggested that salmon from both sides of the Atlantic have a common feeding ground in the general area of Iceland and Greenland. Further evidence for mixing of stocks is provided by data concerning 18 captures from 1961 through 1964 of tagged Canadian salmon between Julianehaab and Holsteinsborg (about 61° to 67° N) along the west coast of Greenland.

Tagging and recapture data pertaining to these 18 fish are given in Table I. All were recaptured from September to November. Nine had been tagged well above tidehead in the Northwest Miramichi River, New Brunswick, as descending, naturally produced smolts. Four were tagged as hatchery-reared smolts of various stocks and released in the Northwest Miramichi and Margaree Rivers at the time of the natural smolt runs (Table I). Another was tagged as a naturally produced smolt in the Grande-Rivière, Gaspé Sud, Quebec. These 14 fish tagged as smolts were at large from 16 to 18 months before recapture. The remaining four fish were first captured and tagged as ascending adults, three at a salmon counting fence on the Northwest Miramichi River and one in Great Rattling Brook on the east coast of Newfoundland. Two of these were tagged as grilse and two as larger salmon. Since these four adult salmon were caught during a spawning run, they probably did not leave the river until late fall or the following spring in which case they spent between 4 and 11 months at sea before being recaptured near Greenland. Each showed a marked increase in length between time of tagging and recapture. Sex and weight are unknown for most of the fish because they were gutted before there was opportunity for examination.

Mr Arne Munch-Ellingsen of Den Kongelige Grønlandske Handel, Sukkertoppen, Greenland, has provided us with valuable unpublished information concerning the fishery for Atlantic salmon near west Greenland. He observed that about 50% of the salmon caught have gonads between 5 and 10 cm long; the remainder have even smaller gonads. It may be concluded that these fish would not have spawned during the season in which they were captured because sexually mature grilse (only 1+ years at sea) have gonads much longer than 10 cm in October.

Nielsen (1961) reported that salmon were frequently caught along the east and west coasts of Greenland. These captures were incidental to a cod fishery

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

TABLE I. Tagging and recapture data pertaining to Canadian Atlantic salmon caught near west Greenland.

Tagging data			Recapture data		
Stock origin (parentage, rearing place),[a] place released	Stage, length	Date	Place	Length, sex	Date
Northwest Miramichi River, New Brunswick	Smolt 14 cm	May 26, 1960	Napassoq Fjord	66.5 cm ♂	Oct. 16, 1961[b]
"	Smolt –	May 24, 1962	Kangâmiut	63.5 cm –	Oct. 20, 1963
"	Smolt –	May 27, 1962	Holsteinsborg	63 cm –	Oct. 21, 1963
"	Smolt 14.8 cm	June 3, 1963	Arsuk	61 cm –	Sept. 24, 1964
"	Smolt –	June 4, 1963	Isua, Julianehaab district	67 cm ♀	Oct. 10, 1964
"	Smolt –	June 4, 1963	Sukkertoppen	64 cm ♀	Oct. 20, 1964
"	Smolt –	June 2, 1963	"	67 cm –	Oct. 22, 1964
"	Smolt –	June 2, 1963	"	69 cm –	Oct. 30, 1964
"	Smolt 15.5 cm	June 3, 1963	"	67 cm –	Nov. 4, 1964
Margaree River stock, Margaree Hatchery, Margaree River, Nova Scotia	Smolt –	May, 1962	Holsteinsborg	68 cm –	Oct. 23, 1963
Late-run Miramichi stock, Saint John Hatchery, Northwest Miramichi River	Smolt –	May 28, 1963	Amerdlog Fjord, Holsteinsborg district	78 cm ♂	Oct. 13, 1964
"	Smolt –	May 28, 1963	Sukkertoppen	72 cm –	Nov. 20, 1964
Chaleur Bay stock, Miramichi Hatchery, Margaree River	Smolt –	June 3, 1963	Arsuk	65 cm –	Nov. 3, 1964

(*Continued*)

TABLE I. Tagging and recapture data pertaining to Canadian Atlantic salmon caught near west Greenland.

(*Concluded*)

Tagging data			Recapture data		
Stock origin (parentage, rearing place), place released[a]	Stage, length	Date	Place	Length, sex	Date
Grande-Rivière, Gaspé Sud Quebec	Smolt –	June, 1960	Kangâmiut	73 cm ♂	Nov. 1, 1961
Northwest Miramichi River, New Brunswick	Grilse 55 cm	July 12, 1960	"	73 cm –	Oct. 30, 1961
"	Grilse 62 cm	Oct. 12, 1962	Holsteinsborg	75 cm –	Oct. 22, 1963
"	Salmon 79 cm	Oct. 16, 1962	Kangâmiut	86.5 cm –	Sept. 9, 1963
Great Rattling Brook, Notre Dame Bay, Newfoundland	Salmon 80 cm	Aug. 5, 1961	Holsteinsborg	95 cm –	Oct.–Nov., 1963

[a]Unless otherwise noted, fish were tagged as naturally produced smolts or adults.
[b]This tag recapture was reported as a News Item in Scottish Fisheries Bulletin, No. 17, June 1962

in these waters. Recently an important fishery for salmon has developed in this area. Hansen (1964; and personal communication) has given the annual catches from 1960 through 1963 as 55, 115, 290, and 420 metric tons (1 metric ton = 2205 lb), respectively. Before the end of the 1964 fishing season the catch had reached 1100 tons. According to Munch-Ellingsen, salmon are caught in nylon nets set out from islands and rocks along the west coast from Julianehaab to Egedesminde (from about 61° to 69°N). The number of fish taken suggests that there are considerable numbers of Atlantic salmon in the eastern part of Davis Strait during late summer and autumn. The tag recaptures indicate diverse origins of these salmon. On the basis of high smolt age of salmon produced in the only Greenlandic river in which *Salmo salar* is positively known to spawn and examination of scales from adults caught off Greenland, Nielsen (1961) concludes that most of the salmon caught near west Greenland come from rivers in which smolt age is lower. The not-too-distant George, Koksoak, and Whale Rivers flowing into Ungava Bay probably do not contribute many salmon to this fishery for their smolt ages are also high (Power, 1961).

It is concluded that in recent years, during late summer and autumn at least, feeding Atlantic salmon from Europe and North America occur together

in considerable numbers in west Greenland waters. Jensen (1939) reported that salmon, previously scarce near west Greenland, were caught there in greater numbers in the mid 1930s. He attributes a change in marine faunal types to long-term temperature changes. This could be a contributing cause of the long-term, large fluctuations of Canadian Atlantic salmon catches noted by Huntsman (1931).

We are grateful to Mr Arne Munch-Ellingsen for details of salmon recaptures and for permission to publish the information he freely gave us. We thank Dr Paul Hansen and Mr Jørgen Nielsen of the Ministeriet for Grønland and Mr E. Gøtze of Gøtze's Reje-og Hummerindustri for sending details of tag recoveries. Mr V. R. Taylor, Chief, Fish Culture Development Branch, Newfoundland Area, Department of Fisheries of Canada, and Dr H.-E. Corbeil, Assistant Director of the Fish and Game Branch of the Quebec Department of Tourism, Fish and Game, kindly gave us permission to publish data concerning the recapture of the salmon tagged in Great Rattling Brook and in Grande-Rivière, respectively. We appreciate the help given in this program by our own field staff who operate our counting fences and tag the salmon.

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

R. L. Saunders
C. J. Kerswill
P. F. Elson

Received for publication August 4, 1964; revised December 30, 1964.

REFERENCES

Allan, I.R.H., and M.J. Bulleid. 1963. Long-distance migration of Atlantic salmon. *Nature*, **200**: 89.

Anonymous. 1962. Long distance migrations by salmon. *Scottish Fisheries Bull.*, No. 17, p. 25.

Carlin, Börje. 1962. Märkt lax återfångad vid Grønland. *Laxforskningsinstitutets, Meddelande*, No. 8, 5 pp.

Cutting, R.E. 1964. Atlantic salmon report. *Maine Fish and Game*, **6**(1): 21.

Hansen, P. 1964. Summary of research work carried out in Subarea 1 in 1963. *International Commission for the Northwest Atlantic Fisheries, Annual Meeting*, June 1964, Serial No. 1403, Document No. 107.

Huntsman, A.G. 1931. The Maritime salmon of Canada. *Bull. Biol. Bd. Canada*, No. 21, 99 pp.

Jensen, Ad. S. 1939. Concerning a change of climate during recent decades in the arctic and subarctic regions, from Greenland in the west to Eurasia in the east, and contemporary biological and geophysical changes. *Kgl. Danske Videnskabernes Selskab, Biol. Medd.*, **14**(8): 1–75.

Kerswill, C.J., and M.H.A. Keenleyside. 1961. Canadian salmon caught off Greenland. *Nature*, **192**: 279.

Menzies, W.J.M. 1949. The stock of salmon, its migrations, preservation and improvement. Edward Arnold & Co., London.

Menzies, W.J.M., and W.M. Shearer. 1957. Long-distance migration of salmon. *Nature*, **179**: 790.

NIELSEN, JØRGEN. 1961. Contributions to the biology of the salmonidae in Greenland I–IV. *Medd. Grønland*, **159**(8): 1–75.

POWER, G. 1961. Salmon investigations on the Whale River, Ungava in 1960 and the development of an Eskimo fishery for salmon in Ungava Bay. *Arctic*, **14**(2): 119–120.

SWAIN, A., W.G. HARTLEY, AND R.B. DAVIES. 1962. Long-distance migration of salmon. *Nature*, **195**: 1122.

SWAIN, A. 1963. Long-distance migration of salmon. *Nature*, **197**: 923.

Ancient Canadian East-Coast Oyster and Quahaug Shells

Over the years we have collected shells of oysters and quahaugs, identified as *Crassostrea virginica* (Gmelin) and *Mercenaria mercenaria* (Linnaeus), in cool-water areas of Canada's east coast where neither of these species is living today. Some of these shells were dark and eroded and all looked very old. Recently we had samples of some of these aged by the radiocarbon method. Merrill *et al.* (1965) report similar collections and ageings of oyster shells from the Atlantic continental shelf between Cape Cod and Cape Hatteras, U.S.A. Their and our results agree very well.

Table I shows that our oyster shells from Georges Bank and Northumberland Strait were 10,600 and 6850 years old[1], and taken from depths of 53 and 37 m. Shepard's figure 1 (1963) indicates that sea levels rose progressively from 20,000 to 3000 B.P. (before present) and that, when our specimens were alive, sea levels were approximately 40 and 15 m below the present level. By simple subtraction, we estimate that our animals lived at depths of 13 and 22 m, respectively. This is well within the depth range of modern oysters but deeper than most. A subsidence of the coast (independent of sea level changes) since our animals died could have produced these high calculated values for depth.

In those times Georges Bank and Northumberland Strait were probably areas of lagoons and shallow seas that warmed quickly in summer. Presumably their annual temperature maxima regularly exceeded the threshold for oyster spawning which in our latitudes ranges from 16 to 20°C (Loosanoff and Nomejko, 1951; Medcof, 1939). This deduction is not inconsistent with Terasmae's (1961) views on climatic changes during this period. His figure 1 suggests that mean temperatures increased in the period 10,000 to 5000 B.P. from about 5° below to about 3°C above present. Thus our findings extend the ancient northward range of oysters and of warm-water conditions beyond that described by Merrill *et al.* (1965).

As the sea levels increased, water temperatures in these areas apparently decreased, and oysters died out leaving our Georges Bank and Northumberland Strait shells in their native beds far from land where they are now taken only in deep dredgings.

Our other three dated collections include two warm-water species, oysters and quahaugs. (Quahaugs spawn at 24–25°C (Nelson, 1928).) None of the samples was found on its native bed. All were found on land where adjacent waters are too cold now for either species to thrive. As a basis for discussing

[1]At press time Mr R. E. Drinnan of the Biological Substation at Ellerslie, P. E. I., advised us that oyster shells taken in Northumberland Strait off Richibucto, N. B., had just been aged at 7335±105 years, B.P. (compare our sample No. 2 in Table I). These shells had been submitted by Dr David Scarratt of the Biological Station at St. Andrews, N. B. They were taken May 26, 1964, by Mr Emile Cormier in a scallop dredge (approximate position, 46°49′N lat; 64°40′W long; approximate depth, 22 m). We deduce that these oysters lived at an approximate depth of 15 m (ageing by Geochron Laboratories, Inc.).

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

them we must assume that those found in middens were gathered alive by Indians from shallow water in the immediate vicinity and that those found on Magdalen Islands beaches were wave-washed from adjacent shallow-water deposits. These three samples were less than 3000 years old — much younger than those from Georges Bank and Northumberland Strait. Their ages ranged from 2175 to 500 years and we believe that their stocks disappeared because of decreases in water temperature at roughly corresponding times.

Shepard's (1963) account suggests no changes in sea levels during the last 3000 years that would have produced a number of drastic, widespread decreases in water temperature. We must therefore look for other causes.

Climatic change, including warmer-than-present periods, has been proposed to us as an alternative explanation. However, Terasmae's summary suggests that mean temperatures in southeastern Canada during the last 3000 years have been below present means except for a short period about 1500 B.P. And even then, the means seem to have equalled but not exceeded present means.

Still another theory is that appearances and disappearances of warm-water stocks were brought about by continuous topographic (erosional) changes of the new shoreline that was created by sea-level rises that terminated about 3000 B.P. These changes probably produced temporary shoal-water areas that warmed sufficiently in summer to be favourable to isolated populations of warm-water species even though the coast as a whole, throughout this period, may have been as unfavourable or more unfavourable than it is today. From time to time many such warm-water pockets may have been created and as quickly destroyed by minor changes in water circulation patterns. And we can assume that after establishing themselves many of the ancient isolated stocks of warm-water species survived precariously pending disasters that finally turned them into beds of fossil shells. We know of stocks that are living on our coast today under just such precarious conditions.

The outer coast of Nova Scotia is barren of oysters now. Nevertheless there is a native oyster population in Ostrea Lake. This lake (44°42′00″ N lat; 63°03′30″ W long) is tributary through a narrow channel to Musquodoboit Harbour, and separated from the cold Atlantic by only an unstable barrier beach.

Another example is Sam Orr Pond (45°09′50″ N lat; 67°02′30″ W long) near St. Andrews, New Brunswick, where the senior author discovered a native population of quahaugs in 1951. This pond occupies a cirque-like depression and lies behind a shallow sill covered by till. The sill protects the pond from being flooded by the cold waters of Passamaquoddy Bay (Bay of Fundy) except at high spring tides.

A break in the barrier beach at Ostrea Lake or slight changes in water level or sill level at Sam Orr Pond could destroy these oysters and quahaugs and leave their shells as relics of extinct stocks to puzzle future geologists. The shore topography of the Magdalen Islands is similarly unstable.

These illustrations show that it is reasonable to postulate that, because of topographic changes during the last 3000 years, there have been times and places about the Magdalen Islands, Que., and Mahone Bay and St. Margaret's Bay, N.S., (see Table I) which favoured oyster and quahaug populations for at least short periods even though neither species lives in these places today. This theory of topographic changes simply explains the presence of the large quantities of oyster and quahaug shells found by Erskine in Indian middens and the wash-ups of oyster shells found by Vass and others (see third entry in Table I) on beaches in the Magdalen Islands. We favour this theory above all others.

The wash-ups are reminiscent of Clarke's (1963a) description of bay scallop shells found on the beaches of Sable Island (43°57′ N lat; 59°55′ W long).

The quahaug shells (last entry in Table I) are from the same site as the periwinkle shells (*Littorina littorea*, Linnaeus) referred to by Clarke (1963b) and dated 700 ± 225 B.P. The dating of our quahaug shells (500 ± 60) conforms well with that for Clarke's periwinkles and therefore offers further support for his conclusion that these snails are indigenous to our coast— not introduced from Europe by settlers within historic times.

TABLE I.

Entry no.	Species and sample no. (McCallum)	Source and depth or site	Radiocarbon age — years before present	Method of collection, collector, and date
1.	Oyster S-186	Georges Bank 42°05′ N lat; 67°15′ W long 53 m	10600 ± 130	Scallop dredge; J. C. Medcof; 1961
2.	Oyster S-185	Northumberland Strait off Murray Harbour, P.E.I. 46°00′ N lat; 62°37′ W long 37 m	6850 ± 100	Hydraulic dredge; J. C. Medcof; 1958
3.	Oyster S-184	Outer east coast of Coffin Island, Magdalen Is., Que. 47°30′ N lat; 61°30′ W long on beach	2175 ± 70	Picked up after storm; Stanley Vass; 1960
4.	Oyster S-183	Whynacht Cove, Mahone Bay, N.S. 44°27′34″ N lat; 64°18′33″ W long on shore	1290 ± 75	Archaeological excavation of Indian midden; J. S. Erskine; 1960
5.	Quahaug S-187	Indian Point, St. Margaret's Bay, N.S. 44°38′40″ N lat; 63°54′55″ W long on shore	500 ± 60	Archaeological excavation of Indian midden; J. S. Erskine; 1960

We wish to thank Professor K. J. McCallum, University of Saskatchewan, for ageing the shell samples; S. E. Vass, Fisheries Research Board of Canada, for contributing the Coffin Island oyster shell collection for study, and Arthur Merrill, U.S. Bureau of Commercial Fisheries, for supplying us with information about his own studies before publication and for helpful criticisms of this paper.

Fisheries Research Board of Canada
Biological Station, St. Andrews, N. B.
J. C. MEDCOF

National Museum of Canada
Natural History Branch
Ottawa, Ontario
ARTHUR H. CLARKE, JR.

Nova Scotia Museum
Halifax, N. S.
JOHN S. ERSKINE

Received for publication September 14, 1964.

REFERENCES

CLARKE, ARTHUR H., JR. 1963a. Variation and subspecific divisions within *Aequipecten irradians* (Lamarck). *Ann. Rept. Am. Malacological Soc.* for 1963, 10.

1963b. Supplementary notes on pre-Columbian *Littorina littorea* in Nova Scotia. *Nautilus*, **77**(1): 8–11.

LOOSANOFF, V. L., AND C. A. NOMEJKO. 1951. Existence of physiologically different races of oysters, *Crassostrea virginica*. *Biol. Bull.*, **101**(2): 151–156.

MEDCOF, J. C. 1939. Larval life of the oyster in Bideford River. *J. Fish. Res. Bd. Canada*, **4**(4): 287–301.

MERRILL, ARTHUR S., K. O. EMERY, AND MEYER RUBIN. 1965. Ancient oyster shells on Atlantic continental shelf. *Science*, **147**(3656): 398–400.

NELSON, T. C. 1928. On the distribution of critical temperatures for spawning and ciliary activity of bivalve molluscs. *Science*, **76**(1730): 220–221.

SHEPARD, FRANCIS P. 1963. Thirty-five thousand years of sea level. *In* "Essays in marine geology in honour of K. O. Emery", University of Southern California Press.

TERASMAE, J. 1961. Notes on late-quarternary climatic changes in Canada. *Annals New York Acad. Sci.*, **95**: 658–675.

Are Killifish Poisonous?

Two species of killifish (also called mummichogs) are common in the Maritime Provinces of Canada — the common mummichog, *Fundulus heteroclitus* (L.), and the freshwater mummichog, *F. diaphanus* (LeSueur). The senior author suspects that under some conditions both may be poisonous to warm-blooded animals, and he has set forth this view with supporting evidence in a manuscript report. In the present paper the junior authors quote from this report, present other evidence that seems pertinent, and discuss the subject.

Common Mummichog

The senior author gives the following account of experiences with this species and some animals that fed on it:

Kingfisher. "In 1927 I fed my first tame kingfisher (*Megaceryle alcyon alcyon* (L.)) largely on sticklebacks and it thrived. After this bird started to fly I began feeding him living common mummichogs from a saltwater pool in Fullerton's marsh near Mount Herbert, Prince Edward Island. On the second day of this diet the kingfisher lost its power of flight. I changed its food back to sticklebacks and it regained its flight. I fed it mummichogs again along with sticklebacks and it became lethargic. After that I gave it no more mummichogs."

Black foxes. "In December that same year, Mr. Ray Atherton of Mount Herbert cut a hole through the ice on the Fullerton marsh and took common mummichogs from a marsh pocket where they were hibernating. He fed some of these to the black foxes (*Vulpes fulva*) in his fox ranch and they all took sick with bloody diarrhoea and refused to eat any more of these fish. Mr. Atherton said that other foxmen had similar experiences and thought the fish were too bony for fox feed."

Crow. "A few days after Mr. Atherton caught his supply of mummichogs I passed the fishing place. There on the ice sat a crow (*Corvus brachyrhynchos brachyrhynchos* (Brehm)) unable to fly. This crow's stomach was full of mummichogs. Many of these fish were still on the ice and they stayed there until the spring break-up without being eaten by other animals."

Ferret. "While at Moser River, Nova Scotia, in 1941, I had a ferret and often fed it fish-suckers, gaspereau, minnows, etc. On one occasion I fed it common mummichogs taken from the estuary. It ate them readily but the next day and thereafter, it refused them, although it continued to eat other kinds of fish."

Reports on the feeding of common mummichogs to a heron and to cats have been made by other observers:

Heron. Our colleague, Mr J. W. Saunders, reports that he maintained a captive great blue heron (*Ardea herodias* (Linn.)) at Ellerslie, Prince Edward Island, from mid August to mid September 1953. On one occasion he fed it approximately 20 common mummichogs taken from Smelt Creek which is the upper part (brackish) of Bideford River. The bird ate these but next morning was prostrate and suffering from severe diarrhoea. It recovered from this and he fed it no more mummichogs.

Cat. Another colleague of the St. Andrews Station, Mrs R. M. Lord, reports that her family at Ellerslie often fed fish to their cats and that the female cats used to catch fish for themselves and their kittens in the shallow riffle where Ellerslie Brook enters Smelt Creek. They ate smelt and trout readily and occasionally would eat common mummichogs, but most of the time they refused this last species.

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

For many years the Biological Station at St. Andrews, New Brunswick, has obtained supplies of common mummichogs from tide pools near the town. The fish are abundant there all spring and summer. Even in February 1964 we dip-netted some fish there from deep holes; these last fish were of at least two size-classes. One (length about 35 mm) was presumed to be the 1963 year-class. The length of the largest fish was 115 mm. The collectors found several of the larger fish dead on the bottom; whether or not they would have been wholesome we could not judge. Herring gulls also congregate there in large numbers at all times of the year, but we have never seen them feeding on these easily available fish. The senior author has made similar observations. He notes that in spring dense spawning schools of the common mummichogs congregate in shallow tide pools but that only on one occasion has he seen a water bird feed on these schooling fish. This bird was a great blue heron. However, stomach analyses (White, 1953, 1957) suggests that herons, terns, kingfishers, and mergansers feed on common mummichogs to some extent.

The senior author views this body of circumstantial evidence as good grounds for suspicion that common mummichogs are poisonous to warm-blooded animals. He also notes that this fish has a yellow spot immediately anterior to the dorsal fin. This spot shows up brighter at spawning time than at other seasons and brightens at any time when the fish is frightened or excited. He speculates that if predators suffer from eating mummichogs the glowing yellow spot might serve as a "warning light" to those types such as wading birds that strike from above. This spot is not mentioned in scientific descriptions of mummichogs to which we have referred.

At this Station we have often used common mummichogs to feed salmon that have been held for long periods in experimental tanks, without apparent ill effects.

As far as we are aware there has been only one test to determine whether common mummichogs are poisonous. On July 17, 1959, samples of this species and the four-spined stickleback (*Apeltes quadracus* (Mitchill)) were taken from the saltwater Sam Orr Pond near St. Andrews. These were macerated and extracted for poison by Mr R. M. Bond of the Fish Inspection Laboratory at St. Andrews. The extracts were bioassayed by Dr A. D. Tennant of the Laboratory of Hygiene, Ottawa, Ontario. The techniques followed were those regularly used in paralytic shellfish poison studies (Prakash, 1963) which involve heat treatment for extraction with tenth-normal hydrochloric acid. The assay results were negative for both species.

This may not have been an appropriate test for mummichog poison if there is such a thing. Thus, whether or not common killifish are toxic or otherwise harmful to warm-blooded animals still invites enquiry.

Freshwater Mummichog

Mergansers. The senior author reports as follows about freshwater mummichogs:

"In 1950–1951 I reared mergansers (*Mergus merganser americanus* (Cassin)) at Petitcodiac, New Brunswick, and fed them small living fish of several species seined from the Petitcodiac River (White, 1957). The birds sometimes ate a few mummichogs but generally killed them and ate them last or refused them altogether. Even when there was no other food they sometimes refused them."

From this, Mr White is suspicious that the freshwater as well as the common mummichog is poisonous. He notes that it has a similar "warning light."

Our colleague, Dr M. W. Smith of this Station, states that his records of stomach analyses show that otter, mink, trout, and bullfrogs feed on freshwater mummichogs, sometimes heavily, with apparent impunity.

The senior author once suggested that the very name "killifish" may suggest some traditional knowledge, perhaps originating during the early period of contact between Indians and Europeans, that mummichogs are dangerous food. But the derivation of the name "killifish" is not clear. The Oxford dictionary suggests that it may have come from "kill" which, in parts of New England, means small stream, or from the fact that mummichogs are used as bait to catch (kill) other fish. Thus, their name does not necessarily imply that killifish are poisonous.

It is true, of course, that some fish are poisonous. The ill effects of some are apparent almost immediately after a single meal (Hubbs and Wick, 1951). Others are damaging to their consumers only after many meals over a long period (Nielands, 1947; Harrington, 1954). We do not claim proof that mummichogs are toxic or otherwise harmful; we merely show that there are grounds for suspicion. On these grounds we would encourage close study using the experimental method. The results would have more than academic interest because mummichogs are used in the laboratory both as experimental subjects and as food for other subject species.

We are grateful to Dr James Stewart of the Fisheries Research Board's Technological Research Laboratory, Halifax, N. S., and Dr E. Chan of the Department of Biology, University of New Brunswick, for their criticisms of this article.

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

H.C. WHITE[1]
J. C. MEDCOF
L. R. DAY[2]

Received for publication July 21, 1964.

REFERENCES

HARRINGTON, ROBERT W., JR. 1954. Contrasting susceptibilities of two fish species to a diet destructive of vitamin B[1]. *J. Fish. Res. Bd. Canada*, **11**(5): 529–534.

HUBBS, C. L., AND A. N. WICK. 1951. Toxicity of the roe of the cabezon, *Scorpaenicthys marmoratus*. *California Fish and Game*, **37**(2): 195–196.

[1]Present address: Petitcodiac, New Brunswick.
[2]Present address: International Commission for the Northwest Atlantic Fisheries, Dartmouth, Nova Scotia.

NEILANDS, J. B. 1947. Thiaminase in aquatic animals of Nova Scotia. *J. Fish. Res. Bd. Canada*, 7(2): 94–99.

PRAKASH, A. 1963. Source of paralytic shellfish toxin in the Bay of Fundy. *Ibid.*, **20**(4): 983–996.

WHITE, H. C. 1953. The eastern belted kingfisher in the Maritime Provinces. *Bull. Fish. Res. Bd. Canada*, No. 97, 44 pp.

1957. Food and natural history of mergansers of salmon waters in the Maritime Provinces of Canada. *Ibid.*, No. 116, 61 pp.

Lesions on the Abdominal Membrane of Lobsters

Brown lesions have been noted on the ventral abdominal membrane of some live lobsters received for our experimental stocks. It was thought that they developed from previous minor injuries. In January 1963, lobsters each with 1 to 3 similar lesions were received from a Charlotte County, New Brunswick, lobster storage pound. The pound manager was concerned about the possible effect of the lesions on survival of lobsters in the pound and the possibility of others being affected. A test was run to obtain information about the cause and possible effects of the lesions on lobsters.

Seven lobsters from the pound with a total of 16 lesions varying from 0.2 to 2.25 cm^2 in area were held for 4 months in close contact with 7 without lesions and with 7 that had been punctured in two places with the rostrum of another lobster. To keep additional injuries to a minimum, both claws of the lobsters were banded with wide rubber bands (Wilder and McLeese, 1961). All 21 lobsters, which varied from 20 to 25 cm total length, were held in a single 58-litre fibreglass tank supplied with running sea water. Water temperature gradually rose from 1.2° to 8.2°C. The lobsters were examined at approximately 2-week intervals.

One-third of the lobsters died over the 4-month period. The experiment was too small to detect moderate differences in mortality and there was no evidence that lesions increased the mortality rate.

Among the group from the pound, 5 of the 16 lesions enlarged during the 4-month period. Both lesions shown in Fig. 1 were about 0.2 cm^2 in area when the lobster was received. One enlarged to about 3.0 cm^2 by 4 months.

All 14 wounds in the punctured group became brown within 10 days. By 4 months, 7 punctures had increased appreciably in area. Punctures that enlarged to about 0.4 and 1.0 cm^2 are shown in Fig. 2. There was no change in any of the lobsters in the group without lesions.

After the observation period, the survivors were held alive but given less detailed attention. Six of these moulted after 7 and 8 months storage. Small lesions healed completely and large ones appeared to be healed, although the new membrane was rough and slightly discoloured. Within a few days, however, the brown discolouration re-appeared and the membrane ruptured. The lobster shown in Fig. 1 is again shown in Fig. 3, 15 days after it moulted. The smaller of the 2 lesions had healed.

Careful examination of 100 freshly caught lobsters and 120 that had been held in tanks for 18 months showed that about one-third of each group had minor lesions but only 5% and 11%, respectively, had lesions large enough to be readily noticeable.

There appears to be little doubt that brown lesions occur at wounds. There was no evidence that mortality was associated with the lesions. However, slight losses could occur in large-scale commercial storage. It is likely

J. Fish. Res. Bd. Canada, **22**(2), 1965.
Printed in Canada.

that the discoloured tissue at lesions is infected with a gram-negative rod bacterium which Baird (1950) found in plug wounds. He showed that injections of this bacterium were lethal to lobsters. Wilder and McLeese (1961) showed that lobsters with plugs were more susceptible to blood disease. Similarly, the broken membrane at a lesion would provide a ready site of entry for *Gaffkya homari*, a bacterium that causes lobster blood disease (Snieszko and Taylor, 1947). Since bleeding was easily started, injury to these areas during commercial storage and shipment could result in death from bleeding.

Fisheries Research Board of Canada
Biological Station, St. Andrews, N.B.

D. W. McLEESE

Received for publication September 14, 1964.

REFERENCES

BAIRD, FREDERICK T. 1950. I. Lobster plugs and their effect on the meat of the lobster claw. *Maine Dept. Sea and Shore Fisheries, Res. Bull.*, No. 2, pp. 2–12.

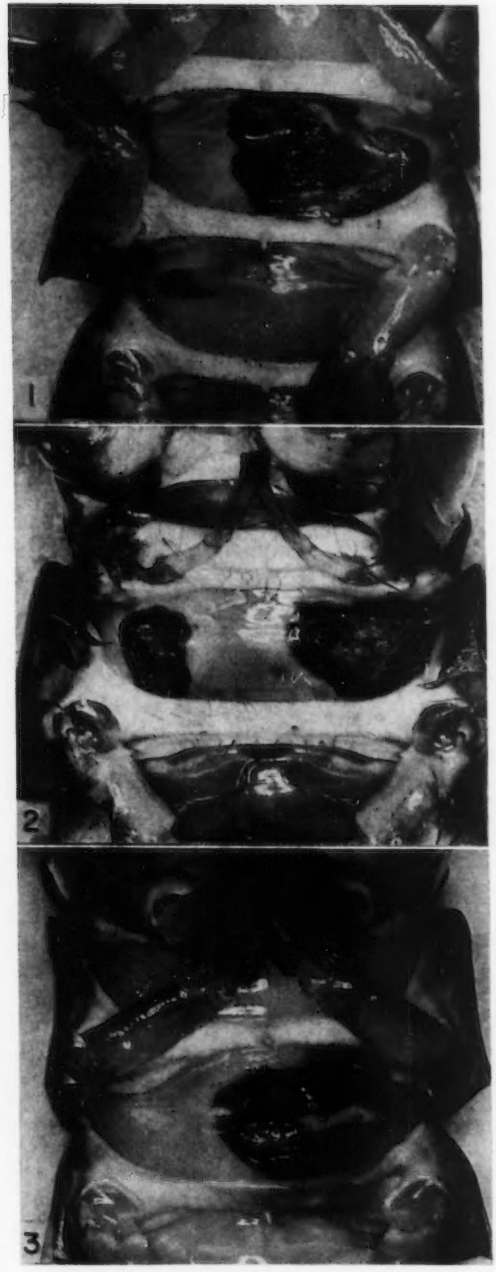
SNIESZKO, S. F., AND C. C. TAYLOR. 1947. A bacterial disease of the lobster (*Homarus americanus*). *Science*, **105**(2732): 500.

WILDER, D. G., AND D. W. MCLEESE. 1961. A comparison of three methods of inactivating lobster claws. *J. Fish. Res. Bd. Canada*, **18**(3): 367–375.

FIG. 1. Two lesions, each about 0.2 cm^2 in area when the lobster was received. One enlarged to about 3.0 cm^2 during 4 months.

FIG. 2. Two punctures that enlarged to about 0.4 and 1.0 cm^2 in area during 4 months.

FIG. 3. The lobster illustrated in Fig. 1, 15 days after moulting, showing that the small lesion healed.



McLeese — J. Fish. Res. Bd. Canada

RECENT ARTICLES ON INVESTIGATIONS OF THE FISHERIES RESEARCH BOARD OF CANADA PUBLISHED IN OTHER PERIODICALS

Studies No.

900. **Smith, G.F.M., and W.E. Ricker.** 1964. Availability of fish. [Federal-Provincial Conference on Fisheries Development, January 20–24, 1964, Ottawa.] Canadian Fisheries Rep., No. 3, pp. 25–29.

901. **Smith, G.F.M.** 1964. Exploration. [Federal-Provincial Conference on Fisheries Development, January 20–24, 1964, Ottawa.] Canadian Fisheries Rep., No. 3, pp. 35–37.

902. **Smith, G.F.M., and A.L. Pritchard.** 1964. Population management. [Federal-Provincial Conference on Fisheries Development, January 20–24, 1964, Ottawa.] Canadian Fisheries Rep., No. 3, pp. 39–42.

903. **Martin, W.R.** 1964. Research on improvement of fishing methods. [Federal-Provincial Conference on Fisheries Development, January 20–24, 1964, Ottawa.] Canadian Fisheries Rep., No. 3, pp. 51–53.

904. **Bligh, E. G.** 1964. Research on quality, processing and products. [Federal-Provincial Conference on Fisheries Development, January 20–24, 1964, Ottawa.] Canadian Fisheries Rep., No. 3, pp. 75–77.

905. **Anon.** 1964. Investigation and management of Atlantic salmon and trout. The research program. Department of Fisheries of Canada, Trade News, **17**(1): 4–11.

906. **Hodder, V.M.** 1964. Prospects for the Newfoundland squid fishery in 1964. Department of Fisheries of Canada, Trade News, **17**(1): 16–18.

907. **Waldichuk, Michael.** 1964. Foams in kraft pulp and newsprint effluents. Parts I and II. Canadian Pulp and Paper Industry, **17**(7): 40–45; **17**(8): 47–51.

908. **Larkin, P.A.** 1964. Canadian lakes. Verh. Internat. Verein. Limnol., **15**: 76–90.

909. **Medcof, J.C., and J.S. MacPhail.** 1964. A new hydraulic rake for soft-shell clams. Proc. Nat. Shellfisheries Assoc. for 1962, **53**: 11–31.

910. **Medcof, J.C., and Neil Bourne.** 1964. Causes of mortality of the sea scallop, *Placopecten magellanicus*. Proc. Nat. Shellfisheries Assoc. for 1962, **53**: 33–50.

RECENT ARTICLES ON INVESTIGATIONS OF THE FISHERIES RESEARCH BOARD OF CANADA PUBLISHED IN OTHER PERIODICALS

Studies No.

900. **Smith, G.F.M., and W.E. Ricker.** 1964. Availability of fish. [Federal-Provincial Conference on Fisheries Development, January 20–24, 1964, Ottawa.] Canadian Fisheries Rep., No. 3, pp. 25–29.

901. **Smith, G.F.M.** 1964. Exploration. [Federal-Provincial Conference on Fisheries Development, January 20–24, 1964, Ottawa.] Canadian Fisheries Rep., No. 3, pp. 35–37.

902. **Smith, G.F.M., and A.L. Pritchard.** 1964. Population management. [Federal-Provincial Conference on Fisheries Development, January 20–24, 1964, Ottawa.] Canadian Fisheries Rep., No. 3, pp. 39–42.

903. **Martin, W.R.** 1964. Research on improvement of fishing methods. [Federal-Provincial Conference on Fisheries Development, January 20–24, 1964, Ottawa.] Canadian Fisheries Rep., No. 3, pp. 51–53.

904. **Bligh, E. G.** 1964. Research on quality, processing and products. [Federal-Provincial Conference on Fisheries Development, January 20–24, 1964, Ottawa.] Canadian Fisheries Rep., No. 3, pp. 75–77.

905. **Anon.** 1964. Investigation and management of Atlantic salmon and trout. The research program. Department of Fisheries of Canada, Trade News, **17**(1): 4–11.

906. **Hodder, V.M.** 1964. Prospects for the Newfoundland squid fishery in 1964. Department of Fisheries of Canada, Trade News, **17**(1): 16–18.

907. **Waldichuk, Michael.** 1964. Foams in kraft pulp and newsprint effluents. Parts I and II. Canadian Pulp and Paper Industry, **17**(7): 40–45; **17**(8): 47–51.

908. **Larkin, P.A.** 1964. Canadian lakes. Verh. Internat. Verein. Limnol., **15**: 76–90.

909. **Medcof, J.C., and J.S. MacPhail.** 1964. A new hydraulic rake for soft-shell clams. Proc. Nat. Shellfisheries Assoc. for 1962, **53**: 11–31.

910. **Medcof, J.C., and Neil Bourne.** 1964. Causes of mortality of the sea scallop, *Placopecten magellanicus*. Proc. Nat. Shellfisheries Assoc. for 1962, **53**: 33–50.

911. **Smith, M.W., and Donald K. Rushton.** 1964. A study of barachois ponds in the Bras d'Or Lake area of Cape Breton, Nova Scotia. Proc. Nova Scotian Inst. Sci. for 1962–63, Part 1, **26**: 3–17.

912. **Mann, D.S., D.W. McLeese, and L.R. Day.** 1964. Salt-water system at the St. Andrews Biological Station of the Fisheries Research Board of Canada, pp. 125–130. *In* Sea-water systems for experimental aquariums. U.S. Fish Wildlife Serv., Res. Rep. No. 63.

913. **Sprague, John B.** 1964. Highly alkaline water caused by asbestos-cement pipeline. Prog. Fish-Culturist, **26**(3): 111–114.

914. **Smith, Michael.** 1964. Synthesis of deoxyribonucleoside-3′,5′ cyclic phosphates by base-catalysed transesterification. J. Amer. Chem. Soc., **86**: 3586.

915. **Hogenkamp, H.P.C.** 1964. Structure and chemical reactions of the cobamide coenzymes. Ann. New York Acad. Sci., **112**(2): 552–564.

Copies of individual reprints, if available, may be obtained from the authors or Board establishments through which the investigations were conducted.

Reprints of these articles are included in an annual volume of "Studies", composed of two parts. These are distributed to a selected mailing list. (Articles numbered 808 to 860 appeared in the Studies for 1963, Part 2.)